EFFECTS OF EXPLOITATION ON THE POPULATION DYNAMICS OF ARCTIC GRAYLING IN THE CHENA RIVER, ALASKA

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EFFECTS OF EXPLOITATION ON THE POPULATION DYNAMICS

OF ARCTIC GRAYLING IN THE CHENA RIVER, ALASKA

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ABSTRACT

An examination of population dynamics and characteristics was used to quantify the effects of a sport fishery on Arctic grayling in the upper Chena River. Comparisons of fish in areas of high and low accessibility to anglers, where accessibility was assumed to be proportional to fishing pressure, revealed that the average size and age, relative abundance, and individual growth rates appeared to decline as a result of fishing, while mortality rates increased.

The circumstantial evidence allows the conclusion that the observed differences in population dynamics and characteristics between sections are, in fact, caused by fishing pressure. Further conclusions are difficult because of the unaddressed questions of differential effects of habitat, migration, and recruitment. This analysis may be used to support the existing management scheme, or to indicate how a desired change may be effected.

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PREFACE

My graduate education, including this research, would not have been possible without the support of many people. I would especially like to thank:

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Reference to trade names does not imply endorsement by the Alaska Cooperative Fishery Research Unit, the United States Fish and Wildlife Service, the Alaska Department of Fish and Game, or the University of Alaska.

To my mother,

Agnes Mary Grabacki,

and to the memory of my father,

Thaddeus Stanley Grabacki

INTRODUCTION

A central question of fishery science, "What are the effects of exploitation (fishing)?", is under continual scrutiny and refinement. The answer is often approached: (1) from a purely biological viewpoint, with Man as a predator depleting a prey; or (2) from a resource management perspective of identifying and attaining some "optimal" harvest. The study of fish population dynamics can help to answer this question; it is this approach to resource management that formed the basis of my investigation.

The Chena River, near Fairbanks, Alaska, was chosen by the Alaska Cooperative Fishery Research Unit as the subject of a comprehensive ecosystem study. Pertinent to my research is an intensive sport fishery for Arctic grayling, Thymallus arcticus (Pallas), along much of the Chena.

The Arctic grayling is the only member of the salmonid subfamily Thymallinae in Alaska. It is characterized by a greatly enlarged dorsal fin, and a small mouth with teeth in both jaws. The maximum size on record was reported from the Katseyedie River, in Canada's Northwest Territories; 75.9 cm (probably fork length), 2.7 kg (Morrow 1980).

The grayling is holarctic in distribution in freshwater drainages from Hudson Bay west to the

Kara and Ob Rivers of northern Eurasia. It occurs throughout mainland Alaska. Lynch and Vyse (1979), noting that the Montana and arctic forms of T. arcticus have been geographically separated for 75 - 100 thousand years, performed an electrophoretic analysis of 36 grayling protein loci. They found that the genetic divergence they observed may be sufficient to warrant sub-specific designations for the two forms. No such distinction has yet been officially made.

Grayling are usually found in the cold, clear waters of rivers, creeks and lakes. They generally avoid turbid waters, but will enter silted glacial streams (Scott and Crossman 1973).

Grayling make a long prespawning migration upstream in spring (late April in Alaska), immediately after ice breakup. After spawning, there is often a second upstream migration to summer feeding grounds. During the summer, individual fish establish territories for surface and mid-depth feeding. In September, grayling move back downstream to overwinter in deep pools (Morrow 1980, Schallock 1966).

The Chena River is a clearwater runoff (non-glacial) stream, typical of grayling habitat in Interior Alaska. It originates at approximately 1100 m (3600 ft) in the low mountains of the Yukon plains section of central Alaska (long. 145° W, lat. 65°N), and flows west for

240 km (150 mi) to the Tanana River, near Fairbanks. The Chena drains about 5130 km^2 (1980 mi^2) of timber and muskeg, and its basin is 160 km (100 mi) long and 65 km (40 mi) at maximum width. The streambed in the pools is mostly clean sand with a few boulders and logs, while heavy rubble and gravel predominate in the riffles and runs (Frey, Mueller and Berry 1970).

The upper Chena, beginning at the Chena River Recreation Area, 42 km (26 mi) on Chena Hot Springs Road, is above the influence of most human activity (mining, logging, wastewater, habitation, etc.), except for recreational fishing and canoeing. Chena Hot Springs Road is the only road access to the upper Chena, paralleling the river for approximately 60 km (37 mi) and passing through the Recreation Area (Figure 1). Parts of the upper river (the North Fork, and the mainstem below the North-East Forks confluence) are therefore readily accessible to anglers. In fact, the Chena River supports the most intensive grayling fishery in the state of Alaska. Annual maxima of 22,700 angler-hours and a total harvest of 18,000 fish have been reported in recent years for the upper Chena alone (Hallberg 1978).

This situation presented parts of the same river system that were physically similar, but widely different in fishing pressure. I compared fish from areas of high and low angler pressure in a rough approximation of a

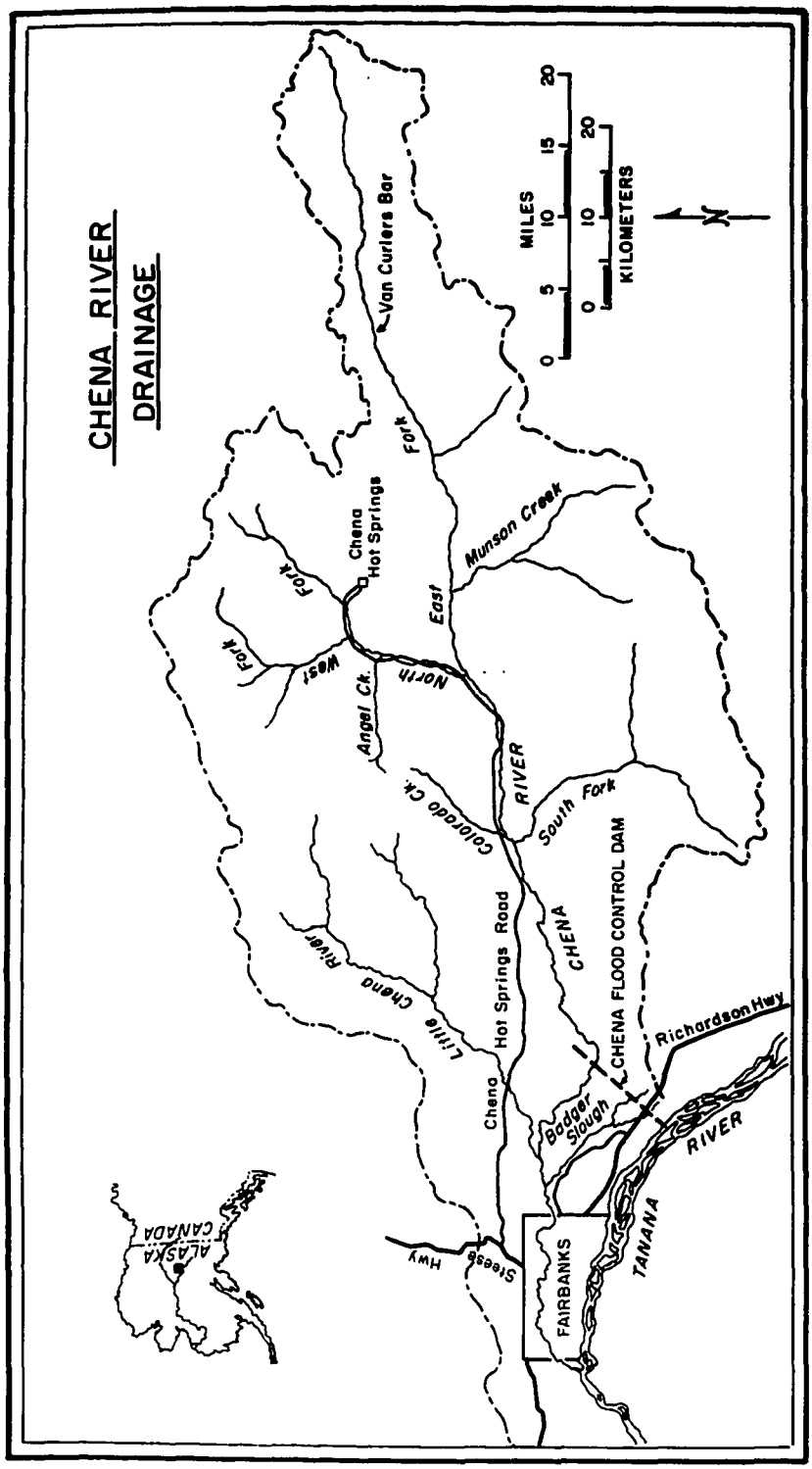

Figure 1 - The Chena River drainage

"treatment and control" experiment. My goal was to address the general hypothesis that fishing affects the population dynamics of upper Chena River grayling so as to decrease the quality of grayling stocks in the more heavily-fished sections. In this general formulation, my working definition of "quality of stocks" included such concepts as abundance, average size, survival, etc.

Other fishery scientists have written that the most immediate and readily observable effects of fishing generally are decreased catches (decreased stock density) and decreased average size in the catch (Bannister 1977, Clady 1967, Cushing 1975, Nikolskii 1969, Watt 1968). However, fishing usually does not cause immediate heavy damage to, or extinction of, the stock; there often, however, is a "fishing up" effect in a new fishery, where the initial high catches of large fish decline and then stabilize (Regier and Loftus 1972).

When a population is not fished, the inputs to the stock of growth and recruitment are equal, in the long run, to the output from natural mortality. This long-term dynamic balance implies that some homeostatic mechanism(s) maintain stock stability. This is the biological basis of the fishery (Schaefer 1968). Fishing adds another output from the stock, in much the same way as the predation portion of natural mortality. In a classic investigation,

Silliman and Gutsell (1958) put forward their "principles of exploitation":

> (A) Any exploitation of a population, however mild, reduces its abundance somewhat.
> (B) Below a certain level of exploitation, fish populations are resilient, increasing their survival and/or growth rates to compensate for the fish removed.
> (C) It is possible, at least with some populations, to raise exploitation rates to the point at which they will cause the extinction of the population.
> (D) Somewhere between no exploitation and excessive exploitation, there lies a level at which the maximum equilibrium yield can be obtained.

When a stock is fished, therefore, it can compensate or not react to the fishing pressure. Conditions of no reaction or negative compensation would mean that fishing could drive the population to extinction. Negative feedback compensatory mechanisms are responsible for the persistence of stocks and species in a density-dependent regulation of stock biomass (Ricker 1977, Nikolskii 1969).

Historical observation and principles of ecological succession indicate that unexploited communities in a stable environment are usually dominated by large, old fish (Regier and Loftus 1972). As a growing fishery takes these older fish, the remaining individuals may compensate physiologically through faster growth, decreased probability of natural death, or increased reproductive output, with a lower age of maturity and/or greater fecundity. Generally, this compensation occurs because of the greater availability of resources after the removal of

the large fish (Tyler and Gallucci 1980). A behavioral (learning) or genetic (selection) compensation may occur as well, such that the catchability of the survivors is decreased, and may be very important in wild ecosystems (Regier and Loftus 1972).

Growth compensation is relatively easy to observe, even though it may not become apparent for the first few years of life (Clady 1967). Indeed, growth often shows a clear inverse relation to stock density, and this dependence becomes more important as the fish increase in age and size (Backiel and LeCren 1978). An increased growth rate was the major response to exploitation of a northern population of lake whitefish (Healy 1980). This increased growth was proportional to the intensity of fishing and resulted in earlier maturation and a shorter generation time.

Some salmonids may comprise an exception to this general rule of compensatory growth in response to exploitation. In view of the strong heritability of growth rate in salmonids, Favro, Kuo and McDonald (1979) stated that a decline in the quality of fishing may be related to changes in the gene pool of a stock caused by selective fishing on the faster-growing individuals. In fact, Falk and Gillman (1974) found no evidence of compensatory growth in Arctic grayling, although they did observe a decrease in individual condition.

Compensatory reproductive output (fecundity) is an important mechanism for exploited salmonids (Jensen 1971), but may not be proportional to the degree of exploitation (Healy 1978a). In general, species with late maturity and/or low fecundity have a small buffer against exploitation (Watt 1968), and fishery management must always allow for adequate reproduction (Nikolsky, Bogdanov and Lapin 1973).

A compensatory decrease in natural mortality may be a response of a stock to exploitation, but it is difficult to quantify since natural and fishing mortality cannot be assumed to be additive (McFadden 1961, Ricker 1975). Mortality may regulate stock size only at the extremes of density, and the density-dependence of mortality decreases as the fish become older and larger (Beverton and Holt 1957, Backiel and LeCren 1978). However, the aggressive territorial behavior of most stream salmonids may make density-dependent mortality more important for them than it is for other species (LeCren 1973).

The ability of a population to replace harvested individuals is often what distinguishes a heavily-fished stock from an overfished stock (Watt 1968), and density-dependent recruitment may be the most important compensatory mechanism in many exploited fish populations (Beverton and Holt 1957). In fact, this type of compensation has been observed to reverse a long-term decline

in yield from the North Sea plaice fishery (Bannister 1977). In theory, the density of recruits must be greater than the density of the parent stock, over some range of parent stock density, in order to compensate for fluctuations in mortality (including fishing), so that extinction is avoided (Tyler and Gallucci 1980). This is the stock's buffer against fishing. However, compensatory recruitment mechanisms are complex, and we do not understand them as well as those of growth and mortality (Backiel and LeCren 1978).

Finally, fishing of one species can often give a competitive advantage to an unfished, or lightly fished, species (Cushing 1975). In one study, brook trout were less able to withstand angling pressure than the brown trout in the same stream; the differences in the age composition of the two species were directly related to innate differences in exploitability (Marshall and MacCrimmon 1970).

I pursued the general goal of investigating the effects of fishing on grayling by comparing grayling population characteristics between areas of high and low angler pressure in the same river system . The characteristics I investigated, and the associated hypotheses, are:

(1) relative abundance: because of removals, grayling will be less abundant in heavily-fished areas;

(2) population structure: because larger (older) fish are more likely to be captured than are smaller fish, these large grayling will be scarce in the heavily-fished areas;

(3) individual growth rate: because of competition, resource limitation, and territoriality, grayling in heavily-fished populations will exhibit a faster, compensatory growth rate;

(4) individual condition: because of this growth compensation, the faster-growing fish in heavily-exploited areas will be in better (plumper) condition;

(5) mortality rate: the addition of fishing mortality to natural mortality will increase total mortality over that of an unfished population. If measureable, the natural mortality rate will show a compensatory decrease, but total mortality will be greater in exploited parts of the river;

(6) interspecific competition: the removal of grayling by angling will allow a competitive increase of round whitefish, Prosopium cylindraceum (Pallas), an unexploited, abundant species.

These are the "alternate", as opposed to the "null", hypotheses.

Recruitment, i.e., the addition of fish to the harvestable stock, is important to fishery management

because it makes possible sustained yields. However, because of the complex nature of recruitment in the Chena grayling stock(s), the estimation of recruitment did not fall within the scope of this study.

Two major obstacles stood in the way of testing these effects of fishing on upper Chena River grayling. The first, and most obvious, question was whether any observed differences between fish populations in two river sections could have been due to factors other than exploitation, i.e., differences in habitat. The second was whether the fish in the arbitrarily-defined areas of the upper Chena were, in fact, separate stocks, or if differential migration based on size or age could explain the differences I observed. I attempted to address these problems as well.

Finally, I considered how the following information and analysis might be used in the management of the fishery.

METHODS

Sites

In 1979, the entire lightly-fished East Fork formed the "control", as compared to the lower North Fork ("treatment") along Chena Hot Springs Road (Figure 2). However, the problems of habitat differences and stock separation did not allow meaningful comparisons between these two reaches of the upper Chena River. The study was modified in 1980 to provide a more tractable design: two pairs of comparisons were formed.

The "control" sections of the upper Chena are not free of fishing pressure, but do differ greatly from the "treatment" sections in their accessibility to anglers. In particular, the upper East Fork above the grass airstrip at Van Curler's Bar (section ABVCB), a mining claim on a large gravel bar, is difficult for the average angler to reach. The fish in section ABVCB were compared with those in the lower North Fork (NF), a physically similar part of the river along Chena Hot Springs Road.

The East Fork is the main tributary of the Chena, and its lower reaches are not substantially changed by the confluence with the smaller North Fork. A second set of comparisons was therefore made between the lower East Fork from Munson Creek to the North-East Forks confluence (MUN)

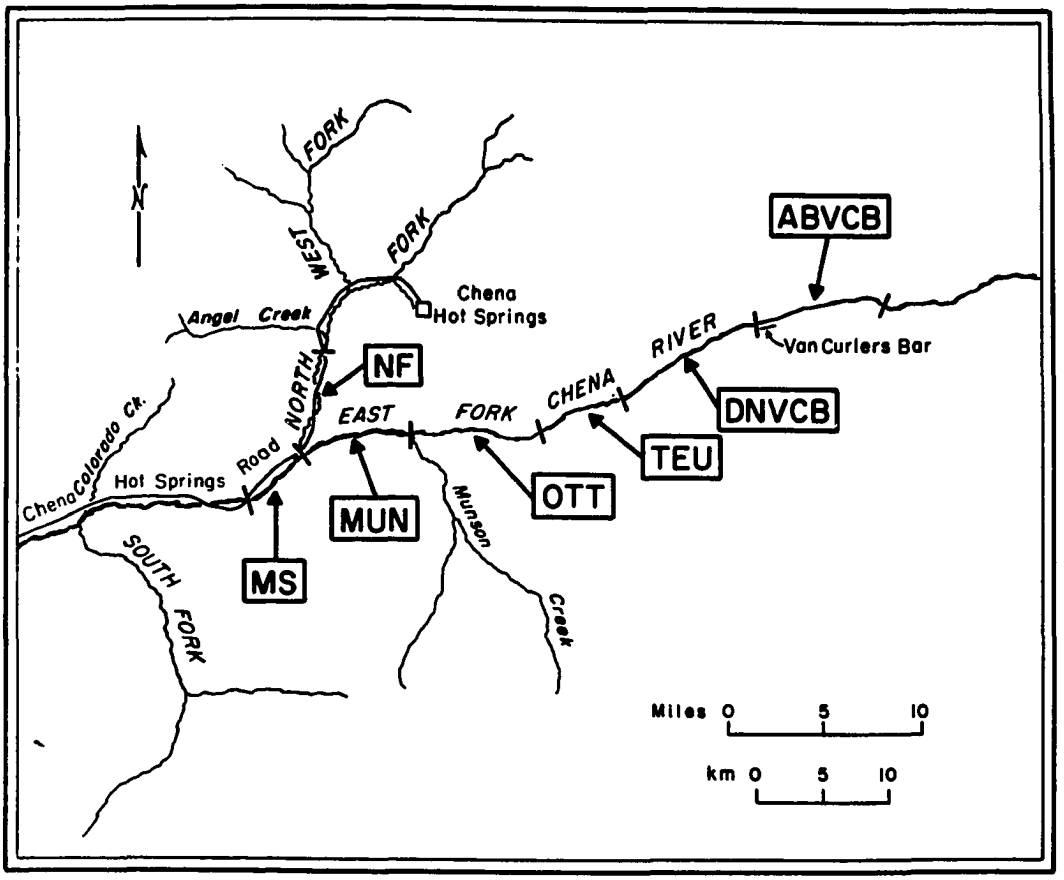

Figure 2 - The upper Chena River, showing the proximity of Chena Hot Springs Road to the North Fork and Mainstem study sections

LEGEND	
Abbreviation	Study Section
NF	North Fork
ABVCB	Above Van Curler's Bar
DNVCB	Downstream from Van Curler's Bar
TEU	Teuchet Creek area
OTT	Ottertail Creek area
MUN	Munson Creek area
MS	Mainstem of the upper Chena

as the control, and the mainstem below the confluence (MS), along the road, as the treatment section.

Travel to and along river sections

Sections of the river along Chena Hot Springs Road were limited by bridges. Anglers involved in this study floated in inflatable rafts between bridges. Helicopters (local air-taxi) provided transport to the upper East Fork. In 1979, we floated by raft to the North-East Forks confluence at the third Chena Hot Springs Road bridge. Gill nets were set overnight at each of the four campsites. In 1980, because interest was focused on the ABVCB section, we were dropped off by helicopter above Van Curler's Bar, and floated the section, angling and setting gill nets. On the next day, we returned by helicopter to the upstream end and floated the section again, angling and retrieving the nets. Fixed-wing aircraft transported us back to Fairbanks from the Van Curler's Bar airstrip.

We used a flat-bottomed aluminum riverboat with an outboard jet unit to travel upstream along the lower East Fork (MUN).

We spent a total of 43 days sampling the four sections in the two seasons (Table 1). Because of lower catches per unit of fishing effort, I concentrated sampling in the exploited sections (NF and MS). We also spent four days sampling each of the other East Fork Sections in 1979.

Table 1 - Length of field seasons, and the number of sampling days in each of the four study sections: North Fork (NF), Above Van Curler's Bar (ABVCB), Mainstem (MS), and Munson (MUN); in 1979 and 1980

Section	1979 First Day	1979 Last Day	1979 Days of Sampling	1980 First Day	1980 Last Day	1980 Days of Sampling
NF	15 Jun	29 Sept	11	29 May	12 Aug	8
ABVCB	29 Jun	14 Sept	4	30 Jun	25 Aug	5
MS	--	--	0	4 Jun	30 Jul	6
MUN	3 Jul	18 Sept	4	24 Jun	15 Aug	5

Capture

Grayling and round whitefish were taken by angling and gill nets, weighed to the nearest gram, and measured (total length) to the nearest millimeter.

Angling (primarily spin, some fly) was performed by a variety of Alaska Cooperative Fishery Research Unit (ACFRU) and non-ACFRU personnel under my supervision. This allowed participation by most ACFRU personnel, but made estimates of angling effort more difficult. Effort was estimated to the nearest angler-day in 1979, and to the nearest angler-hour in 1980. Spinning lures were Mepps and Panther-Martin brands, in sizes 0 and 1, and a variety of colors.

Gill nets were of sinking design and made of green monofilament nylon. Net A was 9.1 m (30 ft) long by 1.8 m (6 ft) deep, with 3 m (10 ft) panels of 2.5, 5.1, and 7.6 cm (1, 2, and 3 in) stretch mesh. Net B was 6.1 x 1.8 m (20 x 6 ft), with 3 m (10 ft) panels of 10.2 and 12.7 cm (4 and 5 in) stretch mesh. Effort was estimated to the nearest day (gill-net-day) for each type of gear.

Both methods captured fish from areas of relatively slow water: pools, eddies, etc. Gill nets were set from shore or from rafts as nearly perpendicular to the current as practical.

Electrofishing methods and longer gill nets were tried and rejected as unsuitable for upper Chena work.

Tagging

In view of the fish damage and tag loss resulting from the use of the common internal anchor tag (Floy number FD-67C), I decided to use the more pliant streamer tag (Floy number FTSL-73), the prototype of which was described by Marullo, et al. (1976). The tags were bright orange, and did not appear to fade during the course of my work. The tags were serially numbered, and printed with: RET ADFG FAI (i.e., Return to Alaska Department of Fish and Game, Fairbanks). The initial difficulty of the split eye of the supplied application needle catching in the fish's flesh was overcome by inserting the tag through the unsplit eye of a larger, sharpened tapestry needle. The tag was then inserted through the dorsal musculature near the insertion of the dorsal fin. All tagged fish were adipose fin-clipped for recognition in the event of tag loss.

The tags were tank-tested on 12 grayling and 12 round whitefish for six weeks, and showed moderate (25%) tag loss for both species.

Tag loss in the field was estimated as the percentage of adipose-clipped fish that were recaptured without a tag.

All live grayling caught by hook-and-line were tagged and released. In the absence of tags, pectoral and pelvic fin-clip codes distinguished grayling from different

sections. Only one of these major fins was clipped for each fish. Approximately 13% of the 977 grayling captured by angling did not survive capture, retention and handling. All fish caught in gill nets (387 grayling, 142 round whitefish) were dead or dying.

Scales

Scale samples were obtained from the left side of the fish between the lateral line and the insertion of the dorsal fin; 5 - 10 scales constituted a sample for each fish.

Scales were soaked for at least eight hours (overnight) in a solution of commercial laundry detergent. The scales were cleaned by toothbrush and/or fingernail, and positioned, sculptured side up, on gummed kraft paper. The paper and scales were placed against 20 mil acetate slides, and this assembly was put inside an aluminum plate - cardboard - aluminum foil sandwich. The scales were pressed, in this sandwich, on a Carver scale press (Model C) at 8.8 mt (20,000 lbs) pressure (applied load) for 30 sec at 93°C (200 °F). One 2.5 x 7.6 cm (1 x 3 in) slide was used for each fish. Slides were stored in the individual scale sample envelopes.

Scale images were magnified on a portable microfiche reader (Bell and Howell "Commuter" Model). I read each scale sample twice, at different times. If these two

readings were unresolvably different, the scales were viewed by a second reader, who was familiar with grayling and round whitefish scales. If disagreement persisted, the sample was removed from calculation. Of the 1103 scale samples read, 13 (1.2%) were rejected; all of these were over age 5. During all readings, the scale envelopes were lifted blank side first, to minimize any bias from fish size or previous reading.

I used standard characters of annulus recognition: crowding, crossing over, discontinuous circuli, etc. Unlike Wyoming grayling (Kruse 1959), the fish of the Chena River seem to form the first annulus at the end of the first year of life (Tack 1971). I therefore interpreted the count of annuli as years of age, with no additions. That is, I found no reason to differ with previous investigators of Chena grayling. Further validity was lent to my technique by the fact that all five fish, irrespective of age, that were tagged in 1979 and recaptured in 1980 showed the expected addition of a single annulus.

Age determination was, of course, easier for younger fish. However, I felt confident of my technique for fish of up to 9 years of age.

Relative Abundance, Sex and Maturity

Relative abundance of grayling was estimated as catch-per-unit-effort (C/f) by angling and in gill nets, based on the assumption that C/f was proportional to absolute abundance. Relative abundance of round whitefish was estimated from gill net catch success, only. Catch per day in net A formed the relative abundance ratios of grayling to round whitefish.

Most dead and dying fish were dissected to determine sex and maturity.

Growth

Back-calculations of length-at-annulus were performed on a programmable calculator, using the Fraser modification of the Dahl-Lea formula (Ricker 1975). Based on previous investigations (Tack 1971) and my own analysis, I used 36 mm as the correction factor for fish length at scale formation.

Length measurements were always expressed as total length rather than as a fork length, as presented in reports by the Alaska Department of Fish and Game (e.g., Tack, Hallberg). I calculated that fork length averaged 0.92 of total length for all grayling in the four sections, in an isometric relation.

Length- and age-frequencies were determined for all grayling in the four study sections, and for grayling

in the middle three sections of the East Fork: downstream from Van Curler's Bar (DNVCB), Teuchet Creek area (TEU), and Ottertail Creek area (OTT) (Figure 2) for the 1979 float trip with greatest catches.

The analysis and comparison of growth rates were approached in a number of ways.

Average lengths at capture by age were compared for grayling and round whitefish in the four study sections. No further analysis was performed for round whitefish. Grayling growth rate analyses included comparisons of:

(1) average length by age at most recent annulus;

(2) back-calculated lengths at annulus for all ages;

(3) growth rate trends within each section;

(4) growth rates for fish of the same age between sections.

Analyses of covariance (Zar 1974) tested the significance of differences in slope for growth rates (3) and (4).

Condition

Fish from each section were grouped into 1-cm total length intervals (e.g., 255 - 264 mm, inclusive, equated to 26 cm), and the arithmetic mean of the lengths in each interval was determined. After a log-log transform, a least-squares linear regression was calculated for individual weights against average total lengths. This

is the procedure of multiple y-values for each x-value (Freund 1971). Analyses of covariance tested for significant differences in slope.

A direct comparison of all ABVCB fish (larger average size) with all NF fish (smaller) would not give a true picture of the differences between the populations. Therefore, the regressions were calculated only in the area of the length-weight curves with "sufficient" overlap: where each length interval for each of the two sections contained at least three fish. In this central range of length intervals, approximately 24 - 35 cm, the numbers of fish in each interval were approximately equal between sections.

Mortality

Age-frequency analysis allowed the development of catch curves for NF and ABVCB grayling in 1979, 1980, and 1979 and 1980 combined; for MS and MUN grayling in 1980; and for NF, MS, and MUN round whitefish in 1980.

The slope of the descending limb of a catch curve allowed estimation of instantaneous total mortality rate (Z) and annual fractional survival (S).

Analyses of covariance tested the differences in slopes. The curves were also examined for differences in the ages over which the mortality occurred.

Physical Factors

Section length, gradient and meander (i.e., sinuosity: the ratio of actual channel length of the section to the straight-line length of the section) were obtained from United States Geological Survey topographic maps (1:63,360, 1954). Since the North Fork section had been channelized since 1954, this meander estimate was obtained from an enlarged high-altitude (National Aeronautics and Space Administration, U-2) photograph.

Estimates of snag (i.e., log jam: potential fish shelter) density and average section width were obtained from projected 35 mm slides taken from an altitude of approximately 305 m (1,000 ft) using a hand-held camera, in September 1980. A snag was defined as any obstruction sufficiently large to develop a pool (hole) behind it, such that the pool was visible in the photograph. Replicate counts of snags along each section were averaged to obtain the estimates.

Average width estimates were also obtained from the 35 mm slides. Scale was taken from objects of known size (bridges and study markers), and by assuming a constant altitude through each section.

RESULTS

Marking, Recapture and Movements

In 1979 and 1980, a total of 606 fish were streamer-tagged and adipose fin-clipped in all seven study sections. Of the 39 recaptured adipose-clipped grayling, 11 (28%) had lost their tags. Apparently, the tank-tests provided a reasonable projection of tag loss in the field.

Of 31 grayling tagged and recaptured in 1979 and 1980 (some fish were recaptured twice), 25 (81%) were recaptured in the section where released (Table 2). Pectoral and pelvic fin-clip codes on 245 grayling distinguished the fish of different river sections in 1979. Of the 20 fin-clipped and recaptured grayling, 15 (75%) showed no upstream or downstream movement upon recapture, in the two field seasons.

Only one tagged grayling and one fin-clipped grayling were recaptured more than one section away from the section of release, throughout this investigation. The time from tagging to recapture varied from one day to 14 months; most recaptures (27; 87%) were taken in the same season as tagged.

Roguski and Winslow (1969) also found that grayling populations were stable throughout a summer, with 61% of their tagged fish showing no movement upon

Table 2 - Movements of tagged and fin-clipped grayling in all seven study sections of the upper Chena River in 1979 and 1980

	Type of Mark	
	Streamer tag	Fin-clip
Number released	606	245
Number recaptured	31	20
Movement upon recapture		
Percentage upstream	6	25
Percentage downstream	13	0
Percentage none	81	75

recapture. In a more lengthy study (Tack (1971), most recaptures occurred in the areas in which the fish were tagged the previous summer.

Sex Ratios and Maturity

Grayling sex ratios were approximately 50:50 in all seven study sections (Table 3). The exception was MS, where the ratio was 34:66, M:F. Van Hulle (1968), however, found that males comprise the majority during the spring spawning run in lower parts of the Chena.

Approximately 50% of grayling were mature at age 5 in the four main study sections (Table 4). This was the same age at 50% maturity as found for grayling in the nearby Goodpaster River, but approximately one-half of the fish in the lower Chena mature at age 4 (Tack 1974).

Comparison of North Fork (NF) and Above Van Curler's Bar (ABVCB) Sections

Section ABVCB was slightly shorter and narrower than NF (Table 5). As might be expected because of its steeper gradient, ABVCB was somewhat straighter and had fewer snags. The most striking difference was accessibility to anglers: NF was along Chena Hot Springs Road, while ABVCB was 44 km from road access.

Catch-per-angler-day was much greater in ABVCB than in NF in 1979 (Table 6). In 1980, however, the more precise catch-per-angler-hour suggested that NF grayling

Table 3 - Sex ratios of grayling, data for 1979 and 1980 combined

Section*	Male:Female	n
NF	55:45	51
ABVCB	48:52	29
MS	34:66	74
MUN	53:47	119
DNVCB	50:50	4
TEU	50:50	40
OTT	60:40	10

* - refer to map (Figure 2)

Table 4 - Percentage of mature grayling by age and sex in the four study sections; data for 1979 and 1980 combined; numbers of individuals in parentheses

Sex	Age	Section			
		NF	ABVCB	MS	MUN
Male	4	0 (9)	0 (2)	0 (20)	4 (25)
	5	50 (8)	50 (2)	67 (3)	12 (17)
	6	100 (3)	100 (1)	100 (1)	63 (8)
	7	100 (2)	100 (1)	-- (0)	67 (3)
Female	4	0 (7)	0 (2)	3 (30)	0 (25)
	5	40 (15)	33 (3)	50 (12)	6 (17)
	6	-- (0)	0 (1)	100 (2)	17 (6)
	7	100 (2)	100 (3)	100 (1)	0 (1)

Table 5 - Physical comparison of North Fork (NF) and Above Van Curler's Bar (ABVCB) sections

	NF	ABVCB
Seasons of study	1979-80	1979-80
Upstream boundary	fifth bridge[a]	flagged tree
Downstream boundary	third bridge[b]	Van Curler's Bar
Length (km)	11.3	9.0
Gradient ($m \cdot km^{-1}$)	2.7	7.0
Meander	1.24	1.17
Snags$\cdot km^{-1}$	4.7	2.4
Average width (m)	12	9
Distance from road (km)	0	44
Means of angler access	automobile foot trail canoe raft	fly-in only: - helicopter - fixed-wing plus walk (no trails)

[a]82 km (51 mi), Chena Hot Springs Road
[b]74 km (46 mi), Chena Hot Springs Road

Table 6 - Relative abundance of grayling based on angling and gill net catch success in North Fork (NF) and Above Van Curler's Bar (ABVCB) sections

	NF	ABVCB
Angling		
Fish·day^{-1}, 1979	5	30
Fish·day^{-1}, 1980	5	10
Fish·hour^{-1}, 1980	3.9	2.9
Gill Nets		
Net A		
Fish·day^{-1}, 1979	5.6	12.0
Fish·day^{-1}, 1980	1.9	3.6
Net B		
Fish·day^{-1}, 1979	0	0
Fish·day^{-1}, 1980	0	1.3

were slightly more abundant. This confusion may result from a day of fishing in NF being shorter than a day of fishing in ABVCB. Catch-per-day estimates in 1980 were similar for the two sections. Gill nets showed consistently higher catch-per-net-day for ABVCB, for both net types in both years. I concluded that grayling relative abundance was greater in ABVCB than in NF.

Ages 5 - 9 predominated in the ABVCB population, while ages 3 - 5 comprised most of the NF population (Figure 3). As might be expected, NF fish were smaller, with most fish falling in the 23 - 29 cm length intervals (Figure 4). Some ABVCB grayling were grouped near the 27 cm length interval, but most ranged between the 35 - 43 cm groups. Age 5, length groups 27 - 32 cm, comprised large portions of both populations. Although angling selected for somewhat larger fish, I saw no differences in the modal groups of the length- or age-frequencies taken by angling or by gill nets.

This preponderance of large fish (34 - 39 cm) in the East Fork has apparently existed for a number of years (Tack 1972). Both Tack (1972) and I also observed a secondary grouping of length frequencies near 25 - 28 cm in the East Fork. Hallberg (1978) found small (17 - 27 cm) grayling in the North Fork along Chena Hot Springs Road, but also encountered larger (34 - 37 cm) fish in the headwaters of the upper North Fork, well above the road.

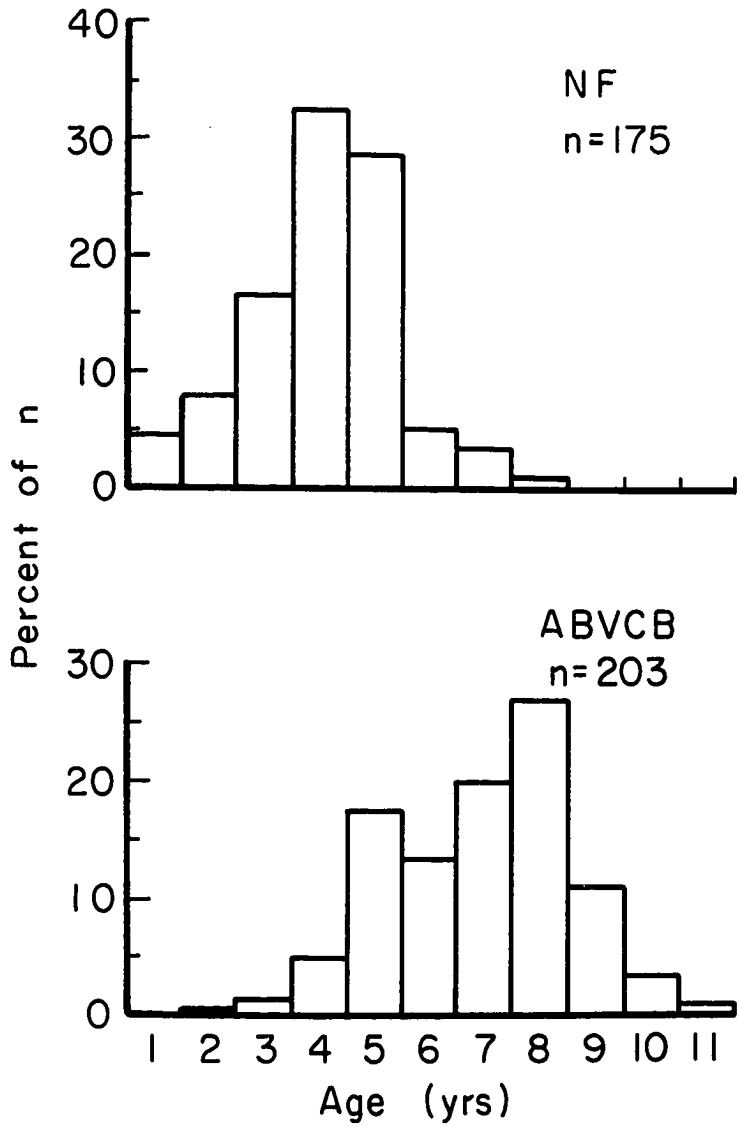

Figure 3 - Relative age-frequencies for grayling in North Fork (NF) and Above Van Curler's Bar (ABVCB) sections; data from 1979 and 1980 combined

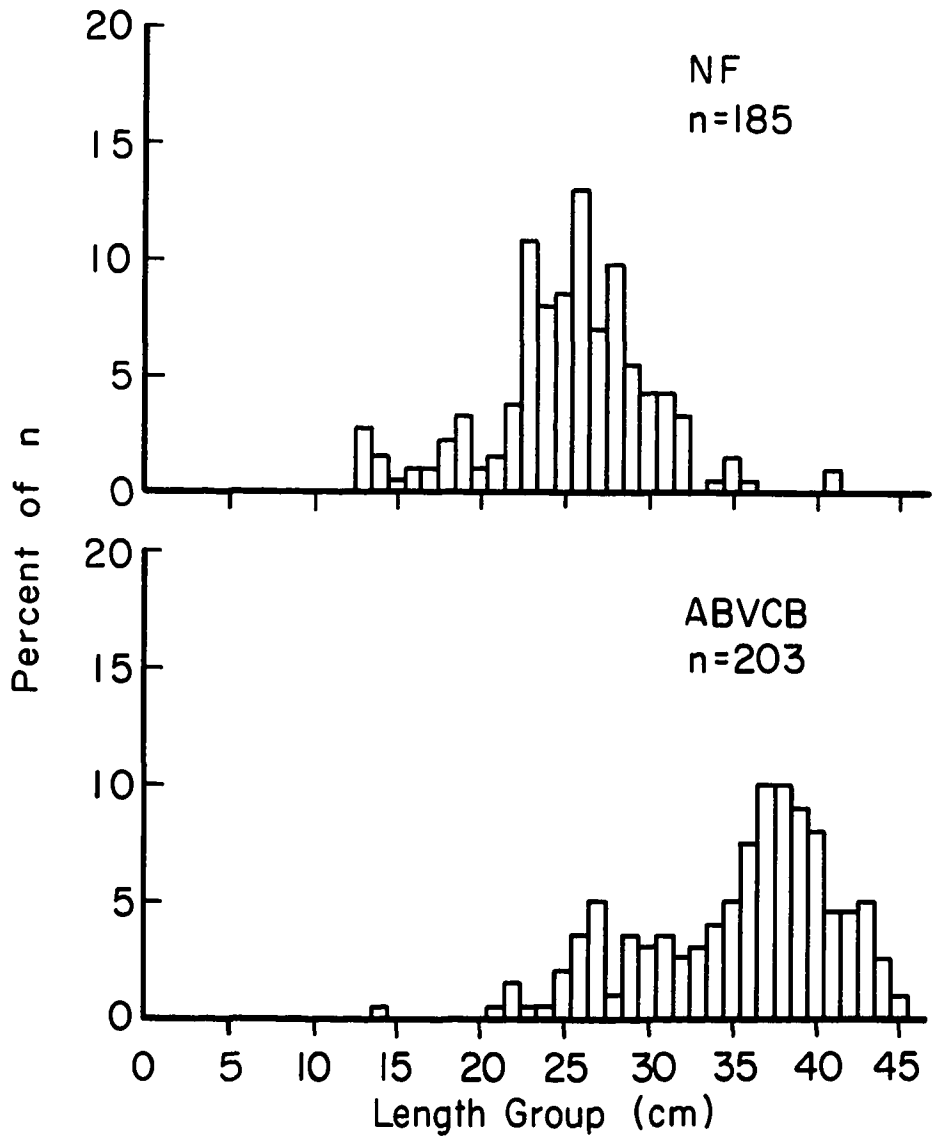

Figure 4 - Relative length-frequencies by 1-cm length groups for grayling in North Fork (NF) and Above Van Curler's Bar (ABVCB) sections; data from 1979 and 1980 combined

Within each section, grayling showed similar average sizes at capture by age between 1979 and 1980 (Table 7). However, ABVCB grayling exhibited faster growth (greater average length at capture for each age) in both years than did NF grayling. Lengths at capture by age were similar to those found by earlier investigators of Chena grayling (e.g., Tack 1976).

Comparison of back-calculated lengths at the most recent annulus for each age, eliminating the variability of averaging lengths over a field season, showed the same trend of faster growth in ABVCB grayling (Figure 5).

A comparison of back-calculated lengths at each annulus for all age groups allowed a determination of whether all fish, regardless of age at capture, tended to be the same length at a given earlier age. The fish in the two sections were all approximately the same size at ages 1 and 2, irrespective of age at capture (Figure 6). However ABVCB grayling of age 3 and above attained an increasingly greater size at age than did NF fish. Further, NF grayling exhibited Lee's phenomenon over given annuli up to age 5; i.e., the older the fish, the less was its back-calculated length at an annulus. However, NF grayling beyond age 6 exhibited reverse Lee's phenomenon, i.e., older fish had progressively greater lengths at any annulus.

Table 7 - Average length (mm) at capture by age for grayling in North Fork (NF) and Above Van Curler's Bar (ABVCB) sections in 1979, 1980, and 1979-80 combined

Age	NF			ABVCB		
	1979	1980	1979-80	1979	1980	1979-80
1	140	131	139	--	--	--
2	217	174	183	136	--	136
3	234	220	230	234	222	226
4	259	253	257	257	244	253
5	280	280	280	286	308	290
6	307	311	310	345	334	340
7	324	355	340	371	375	373
8	--	411	411	392	388	391
9	--	--	--	403	399	402
10	--	--	--	410	425	412
11	--	--	--	--	423	423

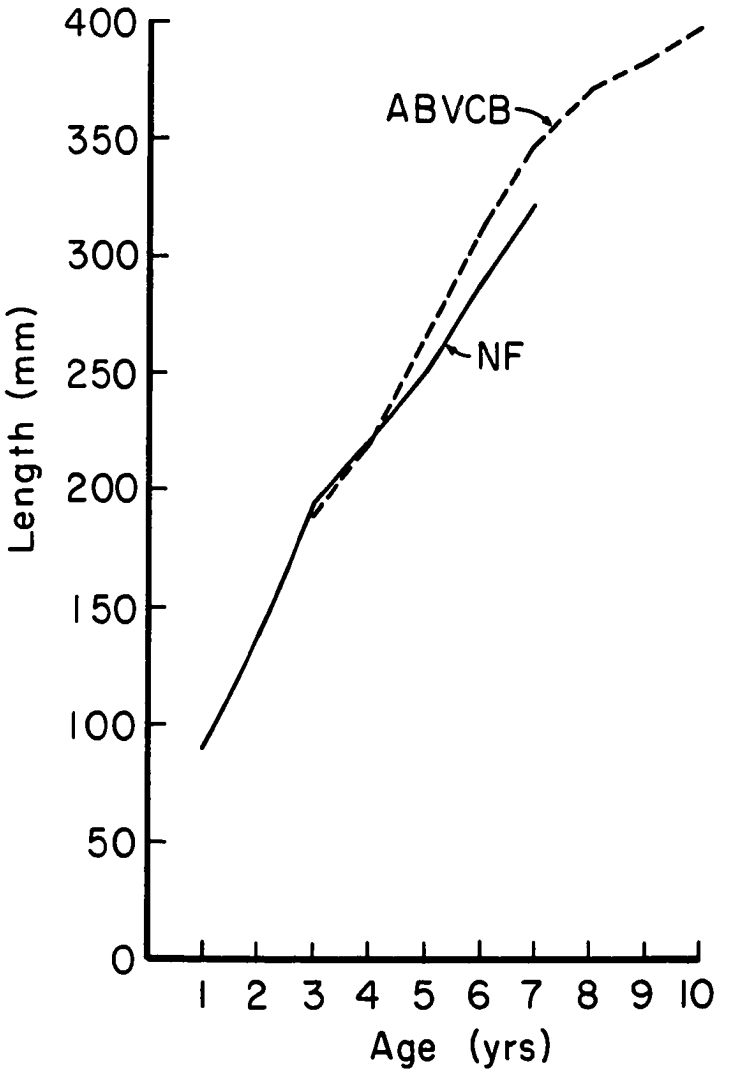

Figure 5 - Back-calculated lengths at the most recent annulus for each age at capture for grayling in North Fork (NF) and Above Van Curler's Bar (ABVCB) sections; data from 1979 and 1980 combined

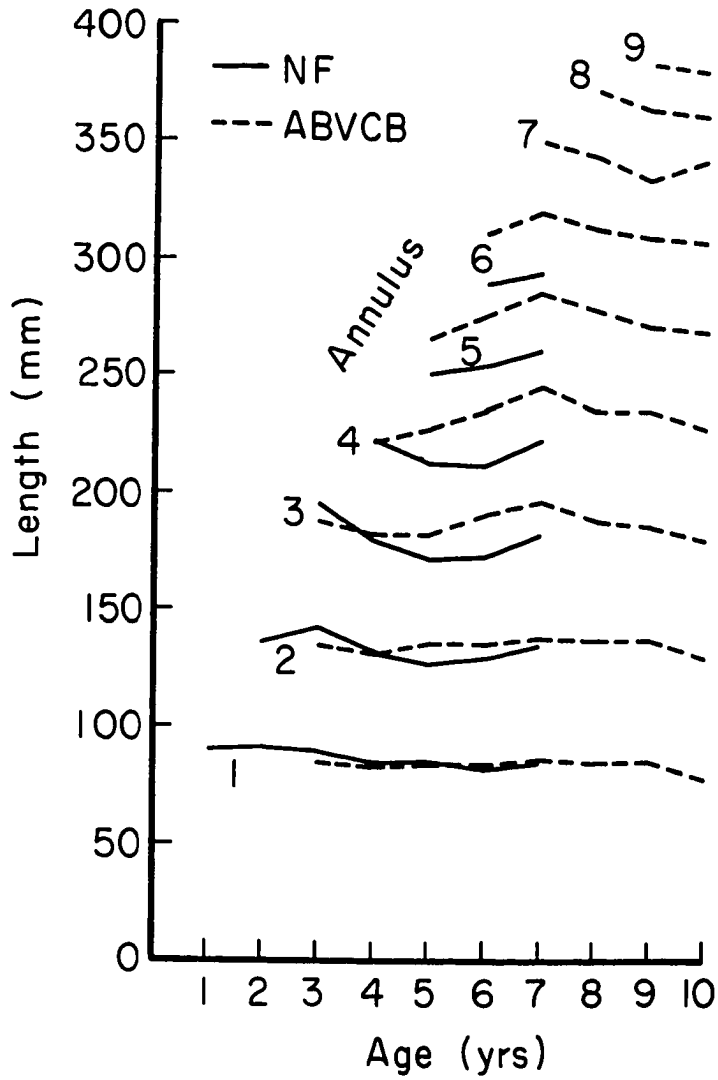

Figure 6 - Back-calculated lengths at annulus across ages for grayling in North Fork (NF) and Above Van Curler's Bar (ABVCB) sections; data from 1979 and 1980 combined

The trend of Lee's phenomenon in ABVCB grayling was opposite that in NF fish (Figure 6). In this section, back-calculated lengths at an annulus steadily increased up to age 7 (reverse Lee's), and thereafter showed a marked decline (Lee's).

This reversal of growth rate trends was more clearly illustrated by comparing growth rates for ages of fish within, not between, sections. Growth rates (back-calculated lengths at annulus) for NF grayling increased between ages 2 - 3, but decreased between ages 3 - 4 and 4 - 5 (Table 8). Then, NF growth rates increased again, albeit weakly, between ages 5 - 6 and 6 - 7.

As mentioned earlier, ABVCB grayling showed the opposite trends. Growth rates increased between ages 4 - 5, 5 - 6, and 6 - 7, but decreased between ages 7 - 8, 8 - 9, and 9 - 10 (Table 9).

The most striking contrasts in growth rates were found by comparing the growth rate of an age group between sections (e.g., NF age 3 vs ABVCB age 3). I found no significant difference ($P > 0.10$) in the slopes of growth curves between NF and ABVCB grayling for ages 3 and 4 (Figure 7). The slopes of growth curves for ages 5 and 6 were significantly greater ($P \leq 0.10$) for ABVCB fish, however. I found no significant difference between the age 7 growth curves, but I think that the lack of significance is due to the small numbers of fish used in this comparison.

Table 8 - Average back-calculated lengths at annulus by age, and direction of change in growth rates between ages at capture for North Fork grayling; data for 1979 and 1980 combined

Age*	Number	Length at annulus (mm) 1	2	3	4	5	6	7	8	Change
1	8	90								
			. . . . .							?
2	14	91	137							
				. . . . .						+
3	29	91	143	195						
					. . . . .					-
4	57	85	133	179	222					
						. . . . .				-
5	50	85	127	171	213	251				
							. . . . .			+
6	9	82	129	173	212	254	289			
								. . . . .		+
7	6	84	135	182	223	260	294	324		
									. . .	?
8	2	90	143	187	225	267	310	357	390	

* At capture

Table 9 - Average back-calculated lengths at annulus by age, and direction of change in growth rates between ages for Above Van Curler's Bar grayling; data for 1979 and 1980 combined

Age	Number	Length at annulus (mm) 1	2	3	4	5	6	7	8	9	10	11	Change
1	0	--											
		. . . . .											?
2	1	81	115										
			. . . . .										+
3	3	84	135	188									
				. . . . .									-
4	10	82	131	181	221								
					. . . . .								+
5	36	83	136	182	227	264							
						. . . . .							+
6	27	83	135	190	235	275	311						
							. . . . .						+
7	41	86	138	196	245	285	321	350					
								. . . . .					-
8	55	84	138	189	236	278	314	346	372				
									. . . . .				-
9	22	85	138	187	235	272	309	336	365	386			
										. . . . .			-
10	7	78	130	182	228	270	308	342	364	382	399		
											. . .		?
11	2	82	122	165	224	261	295	327	352	372	391	404	

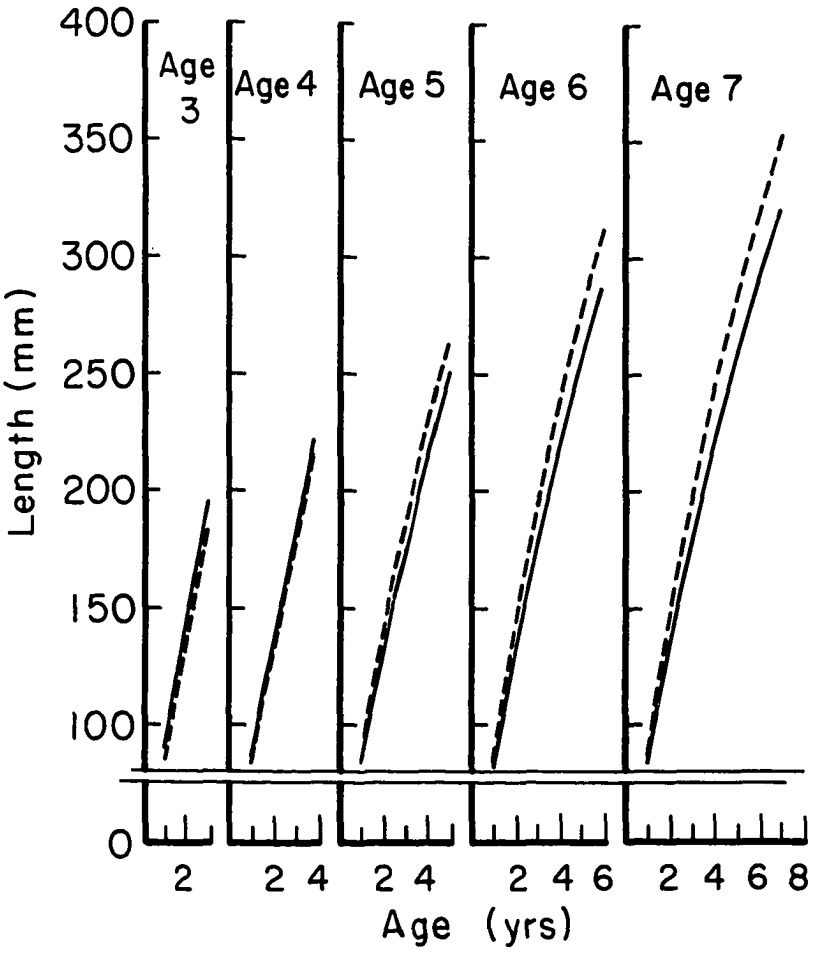

Figure 7 - Age-specific growth rates of grayling in North Fork (-) and Above Van Curler's Bar (---) sections; data from 1979 and 1980 combined

In the range of length groups compared (25 - 35 cm), the length-weight relation for NF grayling, for 1979 and 1980 combined, was:

$\log W = 3.183 \log L - 5.559$, $R^2 = 0.939$, $n = 108$.

The equation for ABVCB grayling, for both years combined, was:

$\log W = 3.194 \log L - 5.588$, $R^2 = 0.964$, $n = 76$.

I found no significant differences ($P > 0.10$) between the slopes or elevations of the two regression lines. The average weights at the average lengths in each length-group used in this comparison were similar (Table 10).

Catch curves showed only small between-year variations in total instantaneous mortality (Z) for NF or for ABVCB fish. Slopes of the descending limbs of the 1979-80 average catch curves were not significantly different ($P > 0.10$) for NF vs ABVCB (Figure 8). The resulting estimates of Z and annual fractional survival (S) were similar (Table 11).

The important difference was not between the numerical values of the mortality rates, but in the ages over which the mortality occurred. Mortality in NF grayling was apparent over ages 5 - 8, but the ABVCB catch curve showed its mortality over ages 8 - 11.

Because the catch curves were similar in slope, but for different ages, the separation of Z into

Table 10 - Average weight at the average length in each 1-cm length group used to compare North Fork (NF) and Above Van Curler's Bar (ABVCB) grayling; data for 1979 and 1980 combined; coefficient of variation for weight in parentheses; coefficients of variation for length were all approximately 1.0

Length Group (cm)	NF		ABVCB	
	Average Length (mm)	Average Weight (g)	Average Length (mm)	Average Weight (g)
25	249.5	120.7 (6.0)	248.3	117.3 (2.7)
26	259.4	134.3 (5.8)	260.6	135.6 (5.0)
27	267.9	146.7 (6.5)	269.8	152.8 (8.9)
28	278.6	165.6 (8.6)	279.3	174.0 (1.6)
29	289.1	186.5 (6.7)	289.1	186.6 (8.9)
30	300.6	218.0 (5.3)	299.2	203.0 (6.0)
31	309.0	225.0 (4.6)	309.7	231.9 (8.7)
32	319.2	260.8 (12.2)	321.4	255.0 (8.7)
33	328.1	-- (--)	328.1	280.3 (3.5)
34	338.8	-- (--)	339.6	318.5 (6.5)
35	350.8	369.3 (4.5)	349.1	344.8 (4.9)

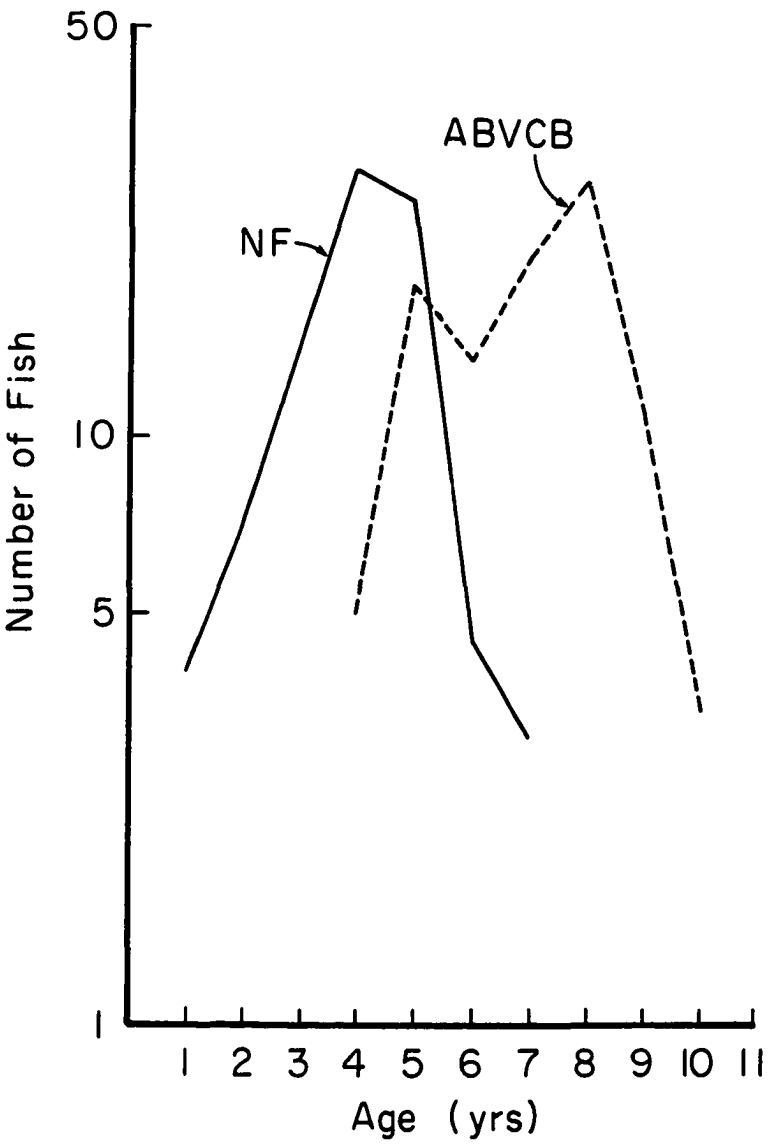

Figure 8 - Catch curves for grayling in North Fork (NF) and Above Van Curler's Bar (ABVCB) sections; data from 1979 and 1980 averaged at each age

Table 11 - Total instantaneous mortality (Z) and annual fractional survival (S) of grayling in 1979 and 1980 in North Fork (NF) and Above Van Curler's Bar (ABVCB) sections

Year	NF		ABVCB	
	Z	S	Z	S
1979	1.04	0.35	1.21	0.30
1980	0.69	0.50	0.68	0.51
1979-80 combined	1.02	0.36	1.11	0.33

instantaneous fishing and natural mortality rates (F and M, respectively), by assuming only natural mortality in ABVCB and additive fishing mortality in NF, was not possible.

In tabulating historical values of S for the grayling from the lower Chena, Hallberg (1978) found between-ages survival ranging from 0.077 to 0.740. My estimates for NF and ABVCB grayling survival are in the middle of this range. Hallberg also noted a sharp decline in survival after age 6 (from an average of 0.52 to 0.13). Geographic separation of our sites, the undefined movements of grayling, and the wide fluctuations observed make comparisons of our mortality estimates untenable.

Comparison of Mainstem (MS) and Munson (MUN) Sections

Section MUN was longer and slightly narrower than MS, and had greater sinuosity (Table 12). Snag density and gradient were similar. The two sections adjoin, so they were not as physically different as NF vs ABVCB, but the disparity in angler access was also not as great.

Angling estimates suggested that MUN had greater relative abundance of grayling, but gill net catches were not very different (Table 13).

Age 4, mostly in length group 25 cm, predominated in both sections (Figures 9 and 10). The MS sample had a higher proportion of younger, smaller fish (none greater than age 7), while some older, larger fish were found in

Table 12 - Physical comparison of Mainstem (MS) and Munson (MUN) sections

	MS	MUN
Seasons of study	1980	1979-80
Upstream boundary	North-East forks confluence	Munson Creek
Downstream boundary	second bridge*	North Fork
Length (km)	8.2	14.4
Gradient ($m \cdot km^{-1}$)	2.2	2.1
Meander	1.19	1.60
Snags$\cdot km^{-1}$	4.8	3.5
Average width (m)	20	15
Distance from road (km)	0	4.5
Means of angler access	automobile foot trail canoe raft jetboat	foot trail jetboat fly-in to Van Curler's Bar

* - 66 km (41 mi), Chena Hot Springs Road

Table 13 - Relative abundance of grayling based on angling and gill net catch success in Mainstem (MS) and Munson (MUN) sections

	MS	MUN
Angling		
Fish·hour^{-1}	2.9	7.2
Gill nets		
Net A		
Fish·day^{-1}, 1979	--	5.0
Fish.day-1, 1980	12.3	17.3
Net B		
Fish·day^{-1}, 1979	--	0.7
Fish·day^{-1}, 1980	0	0

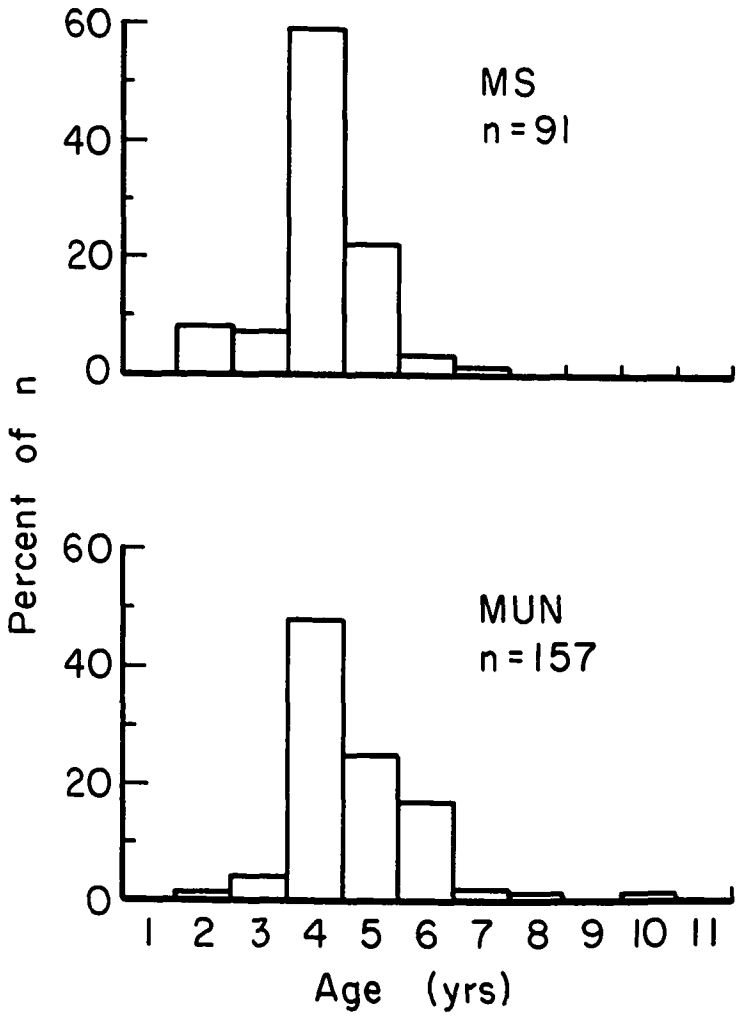

Figure 9 - Relative age-frequencies for grayling in Mainstem (MS) and Munson (MUN) sections; data from 1979 and 1980 combined

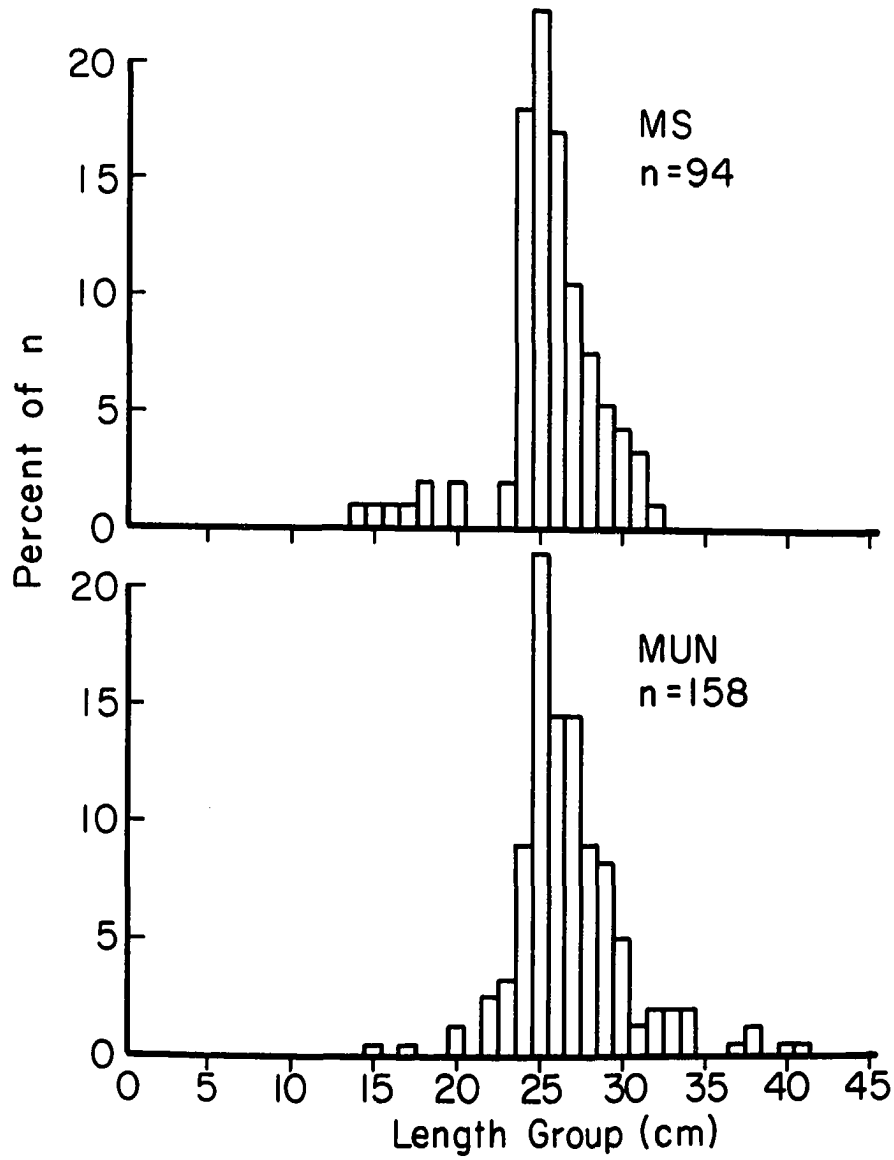

Figure 10 - Relative length-frequencies by 1-cm length groups for grayling in Mainstem (MS) and Munson (MUN) sections; data from 1979 and 1980 combined

MUN. As in the comparison of NF vs ABVCB, angling selected for older fish, but the modal length and age groups were the same in MS and MUN. Tack (1972) also found the peak of length-frequencies for MS grayling to be in the 23 - 26 cm groups.

I saw no apparent differences in length at capture by age between MS and MUN (Table 14). The same similarity appeared in a comparison of back-calculated lengths at the most recent annulus for each age (Figure 11).

I found very few differences in a comparison of back-calculated lengths at annuli across ages (Figure 12), and growth rates showed no trend with age in either section (Tables 15 and 16). Although not statistically different in slope, the growth curve for MS age 3 grayling was significantly greater ($P \leq 0.10$) in elevation than the curve for MUN age 3 (Figure 13). Analyses of covariance revealed no significant differences in the slopes or elevations of the growth rates for ages 4, 5 or 6 ($P > 0.10$).

In the range of length groups compared (24 - 31 cm), the length-weight relation for MS grayling, in 1980, was:

$$\log W = 2.987 \log L - 5.059 \ , \ R^2 = 0.888 \ , \ n = 83.$$

The condition of MUN grayling, in 1980, was:

$$\log W = 2.626 \log L - 4.179 \ , \ R^2 = 0.345 \ , \ n = 131.$$

Table 14 - Average length (mm) at capture by age for grayling in Mainstem (MS) in 1980, and Munson (MUN) in 1979, 1980, and 1979-80 combined

Age	MS, 1980	MUN		
		1979	1980	1979-80
1	--	134	--	134
2	169	--	175	175
3	235	180	219	195
4	254	248	253	252
5	281	283	269	274
6	300	327	304	309
7	285	366	352	361
8	--	370	360	367
9	--	364	--	364
10	--	--	396	--

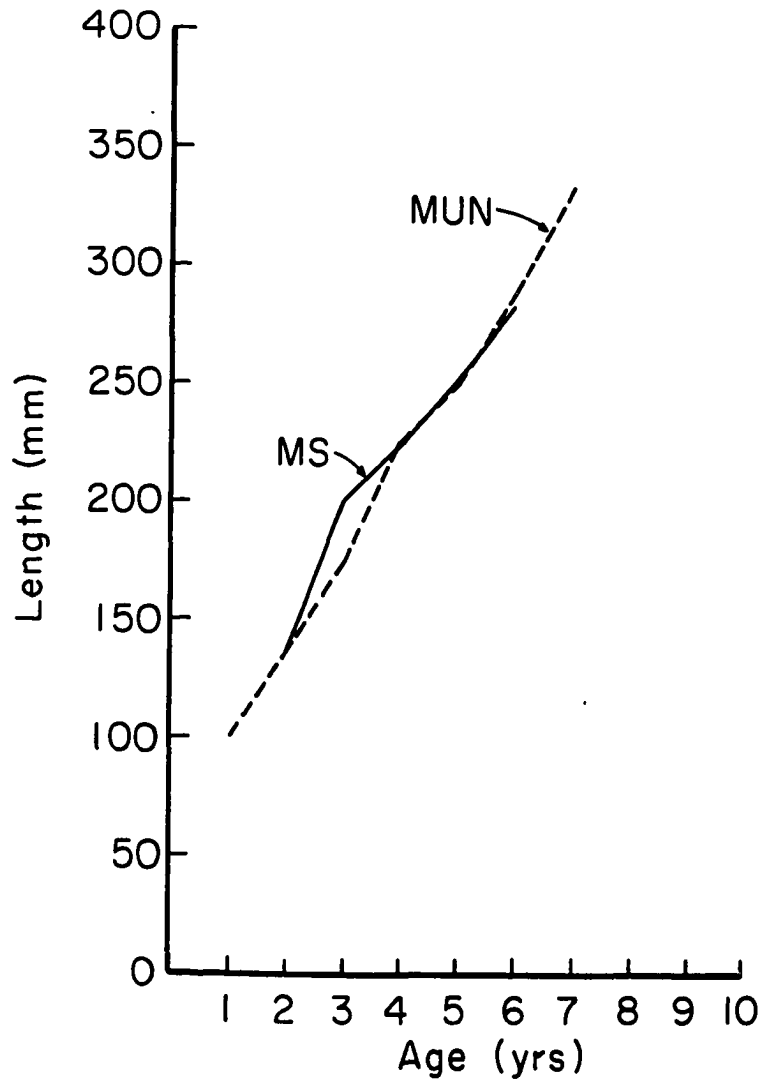

Figure 11 - Back-calculated lengths at the most recent annulus for each age at capture for grayling in Mainstem (MS) and Munson (MUN) sections; data from 1979 and 1980 combined for Munson

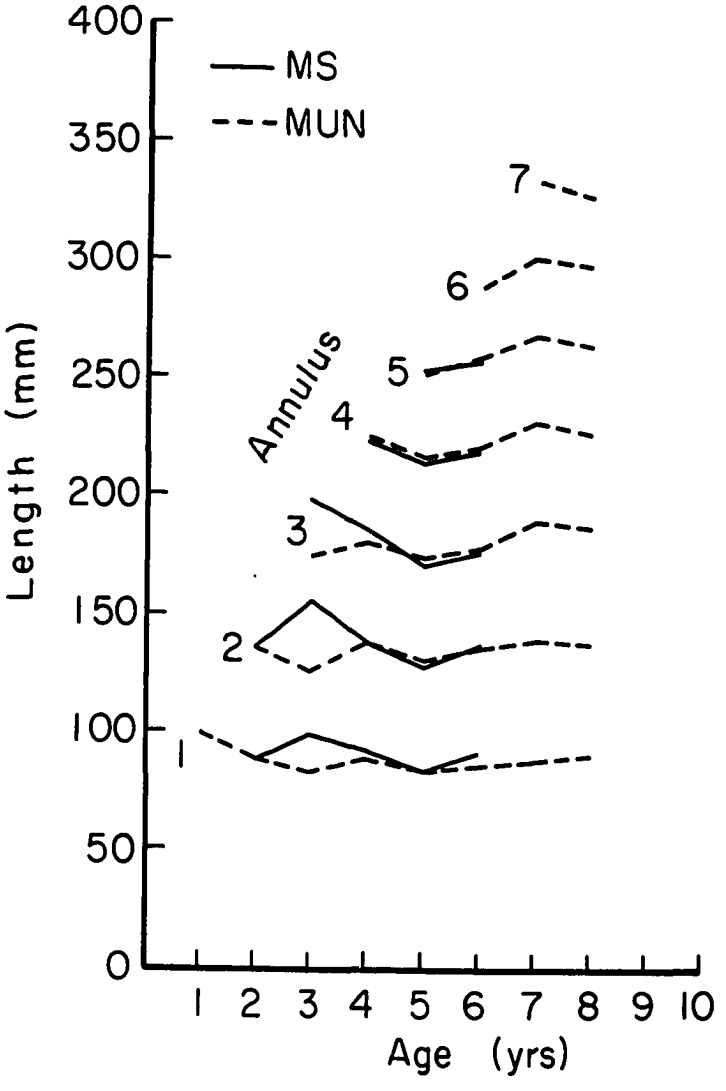

Figure 12 - Back-calculated lengths at annulus across ages for grayling in Mainstem (MS) and Munson (MUN) sections; data from 1979 and 1980 combined for Munson

Table 15 - Average back-calculated lengths at annulus by age, and direction of change in growth rates between ages for Mainstem grayling; data from 1979

Age	Number	Length at annulus (mm) 1	2	3	4	5	6	7	Change
1	0	--							
			. . . . .						?
2	7	88	135						
				. . . . .					+
3	7	99	155	198					
					. . . . .				-
4	53	92	135	185	224				
						. . . . .			-
5	20	83	128	171	214	252			
							. . . . .		+?
6	3	91	138	177	218	258	284		
								. . .	?
7	1	85	137	177	207	227	249	272	

Table 16 - Average back-calculated lengths at annulus by age, and direction of change in growth rates between ages for Munson grayling; data for 1979 and 1980 combined

Age	Number	Length at annulus (mm) 1	2	3	4	5	6	7	8	9	10	Change
1	3	99										?
2	2	88	135									?
3	18	82	125	173								+
4	91	89	135	181	225							-
5	60	82	129	174	216	252						+
6	34	84	135	179	221	258	289					+
7	9	87	139	191	233	268	302	334				-?
8	8	90	137	188	228	265	299	328	350			?
9	1	97	146	190	218	259	292	314	334	350		?
10	1	78	125	160	199	246	275	312	343	362	380	

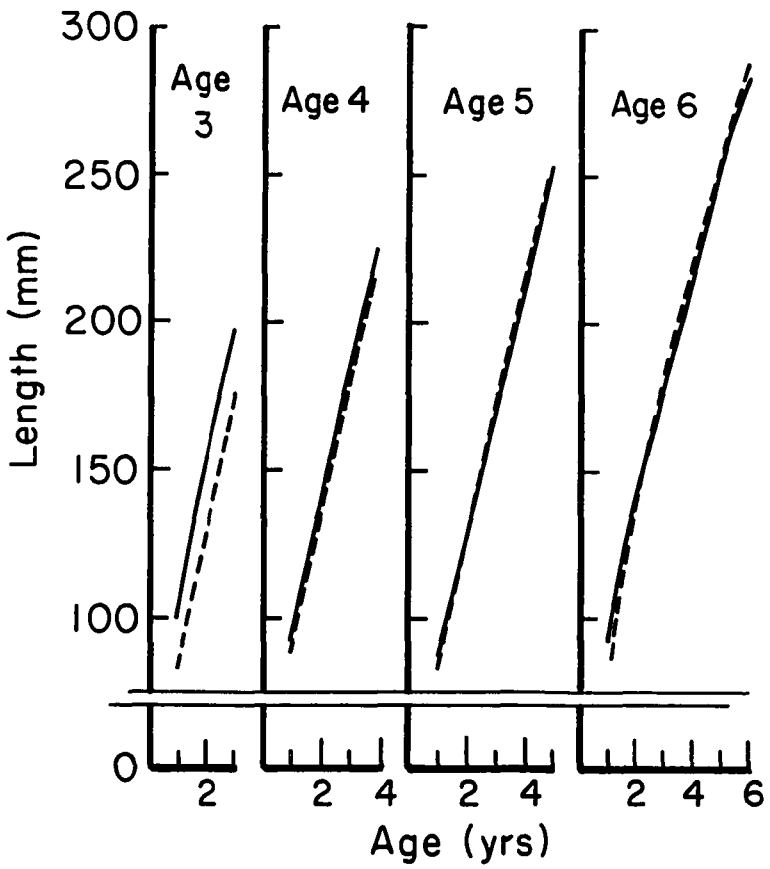

Figure 13 - Age-specific growth rates of grayling in Mainstem (-) and Munson (---) sections; data for 1979 and 1980 combined for Munson

I found no significant difference ($P > 0.10$) between the slopes or elevations of the two regression lines. The slopes appear, however, to be somewhat shallower than those of NF or ABVCB grayling. The average weights at the average length in each length group used in this comparison were similar (Table 17).

Catch curves for MUN for 1979 and for 1980 were too dissimilar to combine into one mortality estimate. The catch curve for MS grayling showed a significantly steeper ($P \leq 0.10$) slope ($S = 0.25$) than did the MUN curve ($S = 0.39$) in 1980 (Figure 14). Further explanation is possible if I assume that: (1) the difference in mortality rates is entirely due to the impact of fishing pressure in MS; (2) fishing was sufficiently low in MUN that Z for MUN represents M, the instantaneous natural mortality rate that would have been observed in MS grayling in the absence of fishing mortality; and (3) instantaneous rates of fishing mortality (F) and natural mortality (M) are additive, summing to Z. If so, then the estimate of $Z = 1.38$ for MS is separable into $M = 0.93$ (= Z for MUN), and $F = 0.45$. The rate of exploitation for MS [$u = F(1-S)/Z$] was 0.24. In 1980, grayling annual fractional survival in the lightly exploited MUN section ($S = 0.39$) was 56% greater than in the heavily-fished MS section ($S = 0.25$) (Table 18).

Table 17 - Average weight at the average length in each 1-cm length group used to compare Mainstem (MS) and Munson (MUN) grayling; data for 1979 and 1980 combined; coefficient of variation for weight in parentheses; coefficients of variation for length were all approximately 1.0

Length Group (cm)	MS		MUN	
	Average Length (mm)	Average Weight (g)	Average Length (mm)	Average Weight (g)
24	240.4	113.4 (7.7)	241.0	114.8 (7.1)
25	249.5	128.4 (8.8)	250.0	127.1 (5.5)
26	258.8	139.8 (8.3)	258.8	135.2 (6.6)
27	268.5	154.0 (5.3)	268.5	152.9 (7.0)
28	277.3	176.0 (7.7)	279.3	176.2 (8.3)
29	288.4	200.7 (6.8)	289.1	196.7 (6.8)
30	295.8	217.7 (3.8)	299.9	220.9 (5.8)
31	310.5	235.5 (7.3)	308.3	236.0 (4.8)

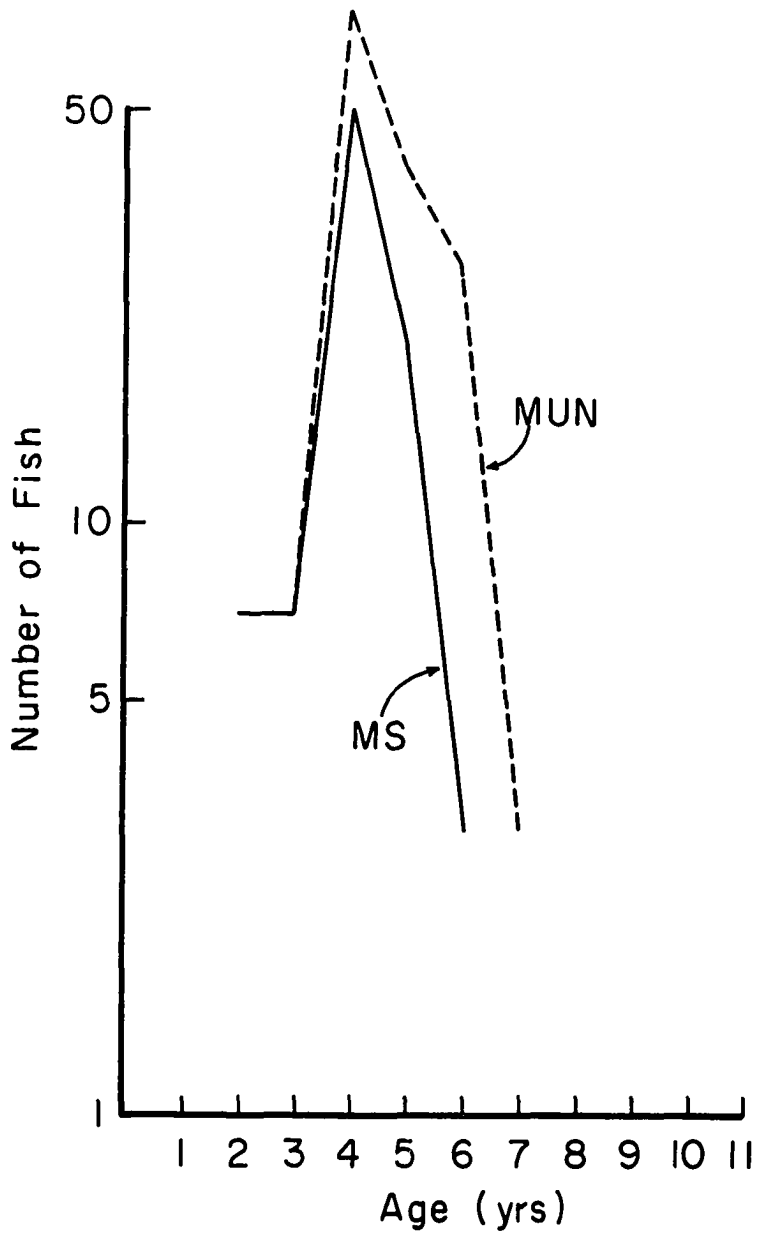

Figure 14 - Catch curves for grayling in Mainstem (MS) and Munson (MUN) sections; data from 1980

Table 18 - Total instantaneous mortality (Z) and annual fractional survival (S) of grayling in Mainstem (MS) and Munson (MUN) sections in 1979 and 1980

Year	MS		MUN	
	Z	S	Z	S
1979	--	--	0.62	0.54
1980	1.38	0.25	0.93	0.39
1979-80 combined	--	--	0.84	0.43

Round Whitefish

Round whitefish were much more abundant in NF than in ABVCB (Table 19). Catches-per-net-day were slightly greater in MS than in MUN.

Ages 5 - 7 comprised large portions of the round whitefish populations in NF, MS and MUN (Table 20). I found no significant difference ($P > 0.10$) in the slopes of length at capture by age among the three sections (Figure 15).

Catch curves for NF, MS and MUN in 1980 were not statistically different ($P > 0.10$) (Figure 16). Since round whitefish are not an exploited species, total mortality is always equal to natural mortality (S was approximately 0.3 for the fish in each section).

Interspecific Competition

Ratios of catch-per-net-day in net A gave indications of any shifts in interspecific competition. The ratios in 1979 and 1980 combined showed that ABVCB had a much greater grayling to round whitefish ratio (26.0) than did NF (1.4). Catch-per-day ratios for 1980 showed very little difference between MS (2.2) and MUN (3.5).

East Fork Grayling and the Problem of Differential Migration

Because of different talents for fishing among ACFRU anglers, measurements of fishing effort (and C/f)

Table 19 - Relative abundance of round whitefish based on gill net catch success in North Fork (NF; average of 1979 and 1980 data), Above Van Curler's Bar (ABVCB; average of 1979 and 1980), Mainstem (MS; 1980) and Munson (MUN; 1980) sections

	Catch·net-day^{-1}			
	NF	ABVCB	MS	MUN
Net A	2.6	0.3	5.7	2.8
Net B	0	0	0	0

Table 20 - Relative age-frequencies of round whitefish in North Fork (NF), Mainstem (MS) and Munson (MUN) sections in 1980; modes are underlined

Age	Percent of n		
	NF	MS	MUN
1	0	0	0
2	0	0	0
3	0	0	3.3
4	6.3	3.0	10.0
5	28.1	<u>33.3</u>	26.7
6	<u>34.4</u>	30.3	20.0
7	21.9	27.3	<u>30.0</u>
8	6.3	6.1	6.7
9	3.1	0	0
10	0	0	0
11	0	0	0
12	0	0	3.3
n	32	33	30

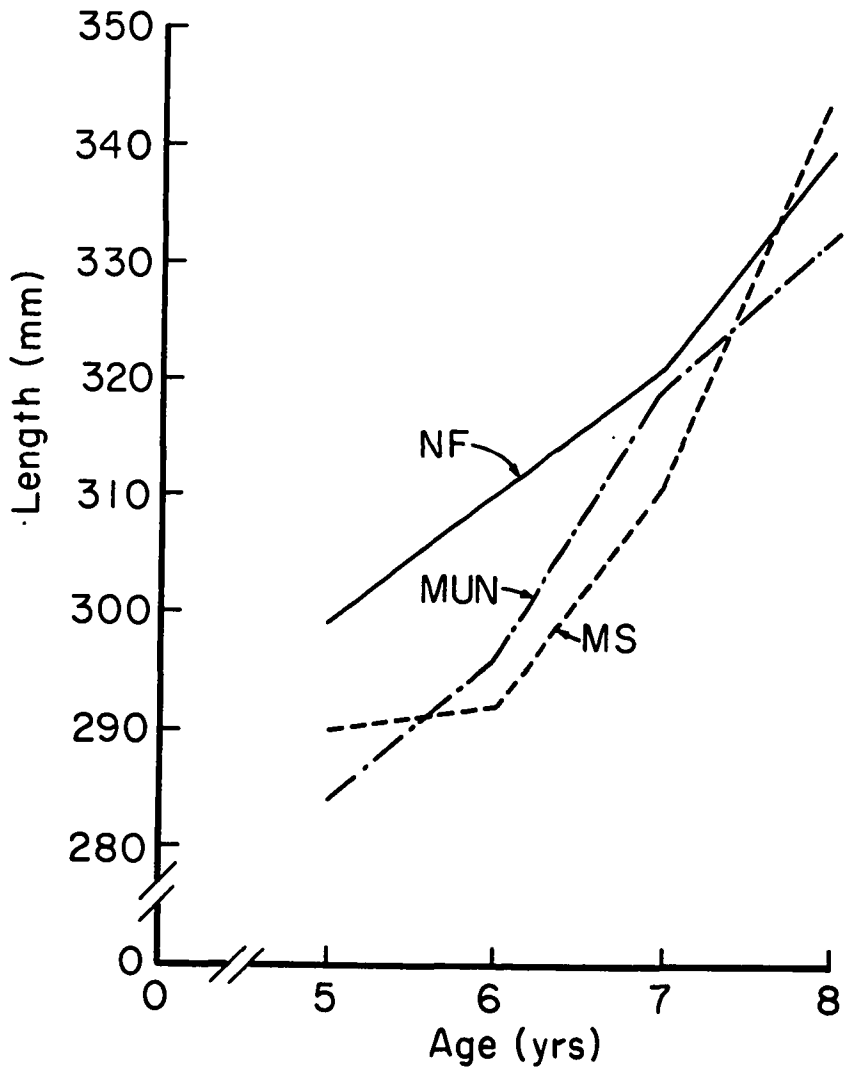

Figure 15 - Average lengths at capture by age for round whitefish in North Fork (NF), Mainstem (MS), and Munson (MUN) sections; data from 1979 and 1980 combined for North Fork and Munson

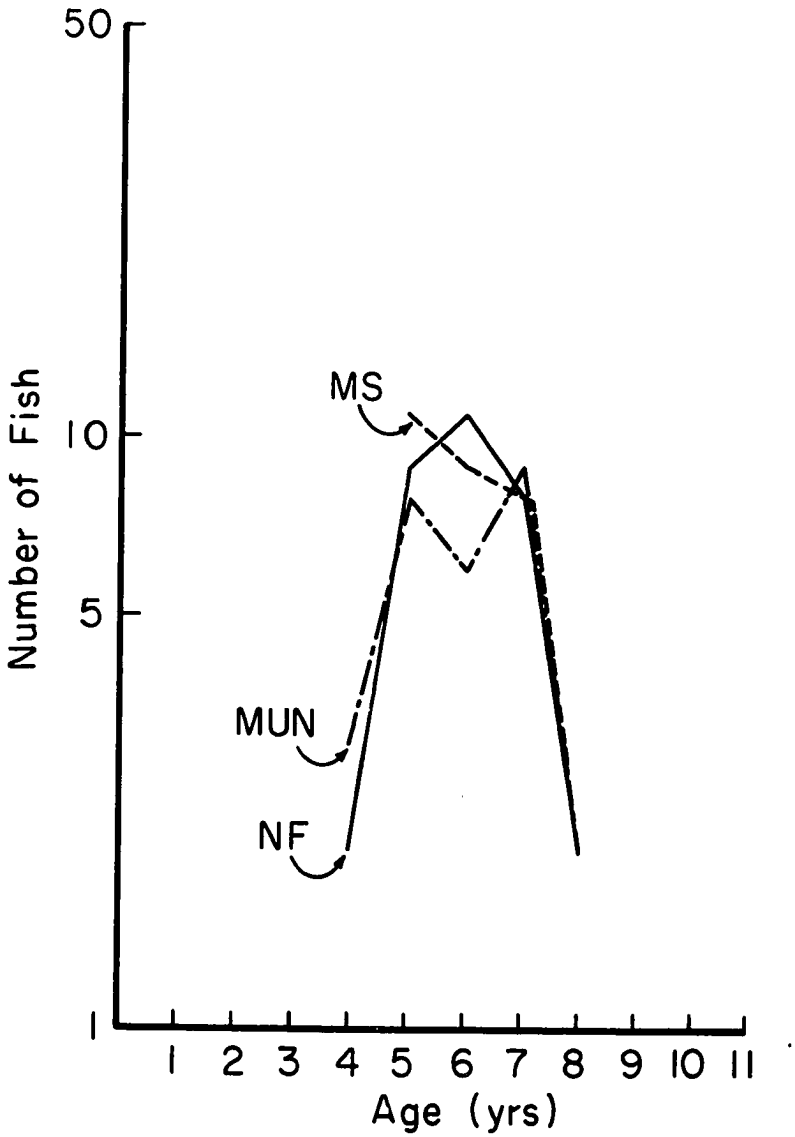

Figure 16 - Catch curves for round whitefish in North Fork (NF), Mainstem (MS), and Munson (MUN) sections; data from 1980

were not comparable between sampling trips. However, one might expect more consistent effort throughout a five-day float trip down the length of the East Fork. Relative abundance estimates (catch-per-day by angling) were therefore comparable within each trip. Averages of angler catch-per-day data for each of the five East Fork sections in 1979 showed that the lowest catches were taken in the extremities (ABVCB and MUN, respectively), and the greatest catches were obtained in the middle sections, particularly in the Teuchet Creek area (Figure 17).

There was a gradient of grayling size and age along the East Fork. The trip of 21 - 25 July 1979 gave the greatest catches, and these were analyzed for size and age structure. Larger, older fish were taken in ABVCB (Figures 18 and 19). As we floated downstream, we caught smaller, younger fish; the smallest and youngest were taken in MUN. Similar gradients of length-frequencies were found in all other East Fork float trips.

Larger, older grayling were found further upstream than smaller, younger fish. In this investigation of the effects of fishing pressure on grayling population characteristics, the lightly-exploited control sections, ABVCB and MUN, were both further upstream than the respective heavily-fished treatment sections, NF and MS. Can differential migration, based on size or age, explain

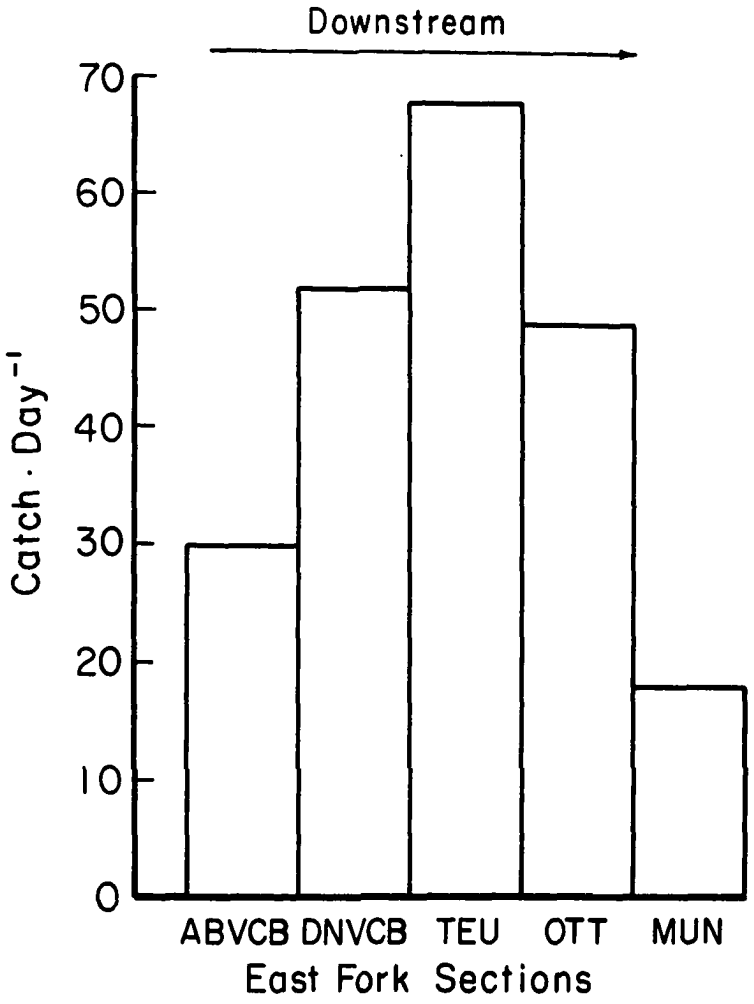

Figure 17 - Relative abundance of grayling based on angling success in the five sections of the East Fork: Above Van Curler's Bar (ABVCB), Down from Van Curler's Bar (DNVCB), Teuchet (TEU), Ottertail (OTT), and Munson (MUN); average catch by all anglers·day^{-1} over the 1979 season

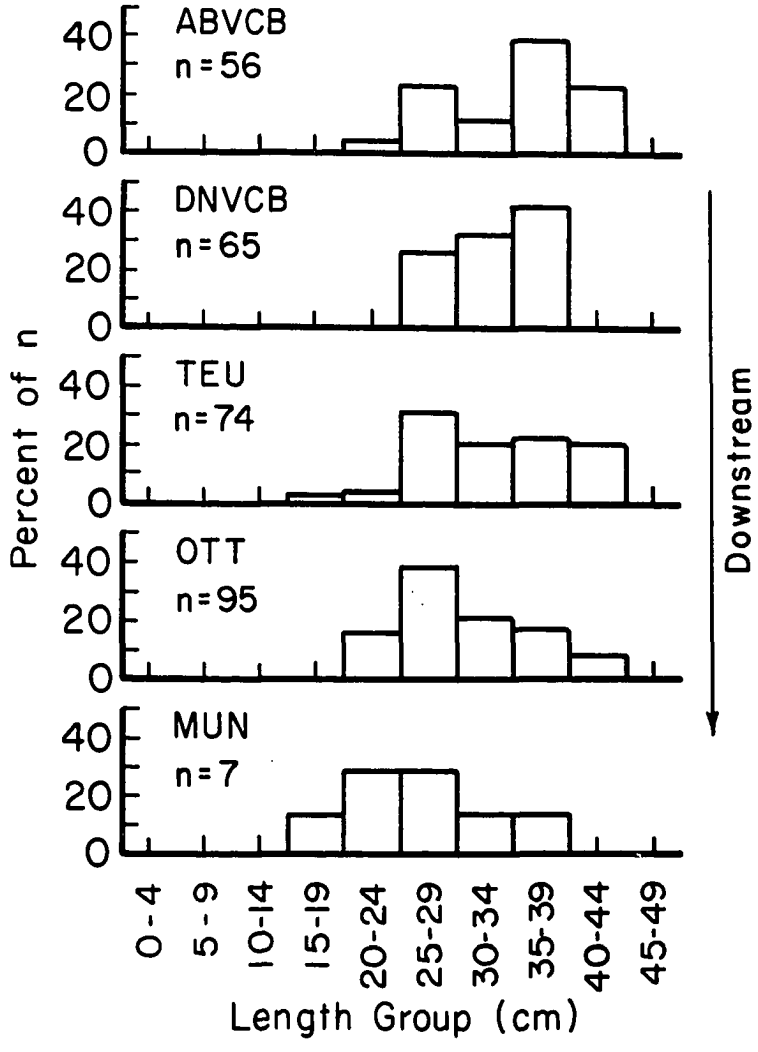

Figure 18 - Relative length-frequencies by 5-cm length groups for grayling in the five sections of the East Fork: Above Van Curler's Bar (ABVCB), Down from Van Curler's Bar (DNVCB), Teuchet (TEU), Ottertail (OTT), and Munson (MUN); data from float trip of 21 - 25 July 1979

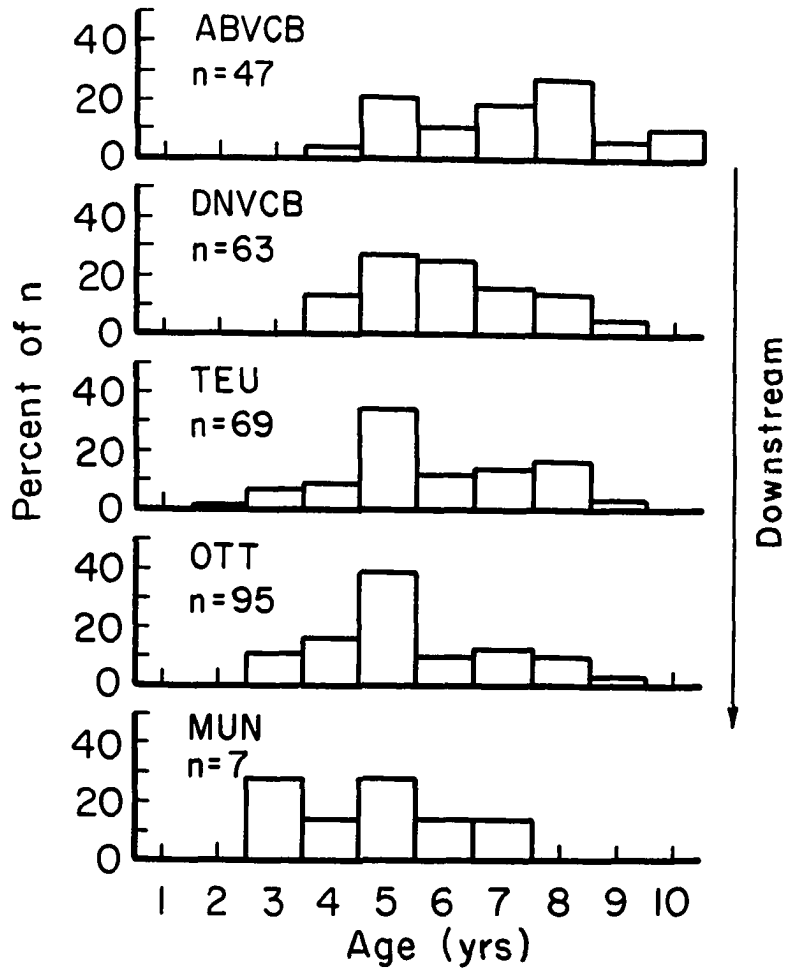

Figure 19 - Relative age-frequencies for grayling in the five sections of the East Fork: Above Van Curler's Bar (ABVCB), Down from Van Curler's Bar (DNVCB), Teuchet (TEU), Ottertail (OTT), and Munson (MUN); data from float trip of 21 - 25 July 1979

the differences I observed between the treatment and control sections?

If differential migration was important in explaining the results of this thesis, I would expect that: (1) faster-growing grayling would be found further upstream in the East Fork than would slower-growing fish; (2) the differences in age-specific survival between the adjacent MS and MUN sections would not be greater than the fraction of marked and recaptured grayling showing movement to an adjacent upstream section; and (3) grayling in the heavily-exploited NF would exhibit faster growth than those in the immediately downstream, and also heavily-fished, MS section. Further, if angling pressure was the same in the two adjacent heavily-exploited sections, MS and NF, then any differences in age-survival between MS and NF populations would represent the effect of migration. However, since MS grayling experience approximately four times the angling effort as do NF fish (Holmes 1981), the effects of migration and exploitation are not completely separable in this fashion.

I did not observe the differences in growth rate that I would have expected if differential migration of grayling was an important part of my explanation. Since the sampling of 25 July 1979 yielded only seven grayling for the MUN section, I combined size and age data from the

samplings of 3 July and 16 August to attain sufficient numbers for a reasonable comparison with other data from the East Fork trip of 21 - 25 July 1979. There was no gradient of age-specific average size along the East Fork (Table 21). Chi-square analyses (Zar 1974) revealed no significant differences ($P > 0.05$) in growth between East Fork sections, for any size or age examined. I saw no consistent difference in growth rates between MS and NF grayling (Table 22).

Examination of grayling age-frequencies obtained by gill net sampling (eliminating the variability and selectivity of angling data) allowed estimation of age-specific survival in adjacent sections. I compared the survival of grayling in any two sections over the same ages along the descending limb of the catch curve.

I found greater differences between the age-frequencies of MS and MUN grayling than differential migration, as reflected in the movements of marked fish, can account for (Table 23). That is, my marking data indicate that 6 - 25% of grayling moved upstream, while the differences between the MS and MUN age-frequencies are 26 - 100%. However, large differences in age-frequencies are also apparent when the grayling of MS and NF are compared (Table 24). This means that differential exploitation and differential migration are not separable in this way, and both may account for these differences.

Table 21 - Average length ($\bar{L}$;mm) at capture by age (yrs) for East Fork grayling, 21 - 25 July 1979; standard deviations (s) and sample sizes (n) follow each $\bar{L}$

Age at Capture		ABVCB (upstream)	DNVCB	TEU	OTT	MUN (downstream)
4	$\bar{L}$	257.2	262.8	262.0	249.7	247.3
	s	19.6	16.0	21.2	12.5	24.7
	n	5	8	5	15	15
5	$\bar{L}$	275.6	294.6	287.7	281.8	283.1
	s	12.8	24.7	17.4	24.5	26.0
	n	11	17	24	37	20
6	$\bar{L}$	336.6	330.9	346.4	332.8	327.0
	s	27.8	19.8	16.3	17.8	35.7
	n	5	16	8	9	7
7	$\bar{L}$	360.8	363.8	371.7	367.4	370.3
	s	15.9	13.4	49.4	22.1	16.0
	n	11	10	10	12	3

Table 22 - Average length ($\bar{L}$;mm) at capture by age (yrs) for grayling in Mainstem (MS) and North Fork (NF) sections in 1980; standard deviations (s) and sample sizes (n) follow each $\bar{L}$

Age		MS	NF
2	$\bar{L}$	169.1	173.7
	s	18.3	12.4
	n	7	11
3	$\bar{L}$	235.4	219.6
	s	17.2	24.0
	n	7	7
4	$\bar{L}$	253.6	253.2
	s	11.4	16.2
	n	53	20
5	$\bar{L}$	280.7	280.4
	s	19.9	21.6
	n	20	18
6	$\bar{L}$	299.7	311.2
	s	23.1	28.6
	n	3	6

Table 23 - Absolute and relative age-frequencies for grayling in Mainstem (MS) and Munson (MUN) sections in 1980, and percentage difference in relative age-frequencies, showing how much more abundant the fish of a given age are in MUN; relative age-frequencies were calculated only over those ages used in comparing the catch curves for the two sections

Age	MS		MUN		Percent Difference*
	n	%	n	%	
4	49	71	49	50	-42
5	16	23	31	31	26
6	3	4	14	14	71
7	1	1	3	3	67
8	0	0	2	2	100

*(MUN % - MS %)/MUN%

Table 24 - Absolute and relative age-frequencies for grayling in Mainstem (MS) and North Fork (NF) sections in 1980, and percentage difference in relative age-frequencies

Age	MS		NF		Percent Difference*
	n	%	n	%	
5	16	80	11	61	-31
6	3	15	3	17	12
7	1	5	2	11	91
8	0	0	2	11	100

*(NF % - MS %)/NF%

Further comparisons of MS and NF populations may help to separate the effects of exploitation and migration. Estimates of relative abundance of grayling based on angling success in the two sections are not very different (Table 25). However, gill net catches indicate a much greater grayling abundance in the more heavily-fished MS section. Although ages 4 and 5 predominate in both sections, the upstream NF section has more small, young fish of ages 1 - 3, and sizes 14 - 23 cm (compare Figures 3 and 9, and 4 and 10).

Table 25 - Relative abundance of grayling based on angling and gill net catch success in Mainstem (MS) and North Fork (NF) sections in 1980

	MS	NF
Angling		
Fish·hr^{-1}	2.9	3.9
Gill net		
Fish·day^{-1}		
Net A	12.3	1.9
Net B	0	0

DISCUSSION

Classical fishery science holds that fishing usually changes one or more characteristics of the exploited population. Many of these in Chena grayling exhibit the expected shifts (Table 26). I will discuss these changes with respect to exploitation, and then examine the soundness of my conclusions in regard to differential migration.

Estimates of relative abundance based on angling success were confusing, and in some cases, contradictory. This was caused by differences among the anglers participating in this study, and between gear types (spin and fly). Relative abundance estimates based on gill net catches were more consistent and reliable. These estimates indicate that grayling abundance in unfished areas was greater than or equal to that in more accessible sections. This lends some support to the alternate hypothesis that fishing decreased grayling abundance; the greater decrease was found in the comparison of the two more widely separated sections (NF and ABVCB).

There was a striking difference in population size and age structure between NF and ABVCB. A lesser, but nevertheless important, difference was observed between MS and MUN. In both comparisons, the accessible sections contained relatively fewer large, old fish than did their less accessible counterparts. Both comparisons supported

Table 26 - Qualitative summary of results: the apparent impact of exploitation on grayling population dynamics and characteristics in North Fork (NF) as compared to Above Van Curler's Bar (ABVCB) sections and in Mainstem (MS) as compared to Munson (MUN) sections

Characteristic	Impacts of exploitation in: NF as vs ABVCB	MS as vs MUN
Relative abundance	decrease	none
Average size	decrease	decrease
Average age	decrease	decrease
Individual growth rate	decrease	none
Condition	none	none
Mortality	increase	increase
GR:RWF	decrease	decrease

the alternate hypothesis that fishing decreased the population's average size and age, with greater support in the NF vs ABVCB experiment.

Strong differences were found in the growth rates of NF and ABVCB grayling. The fish in both sections started out at the same size at early ages, but ABVCB grayling showed increasingly faster growth thereafter. More precisely, it seems that faster growing fish survived harvest to be caught in my gear in ABVCB, but not in NF. These observations support neither the alternate hypothesis of faster growth in the fished area nor the null hypothesis; instead, the results are the reverse of what was expected. It seems that the NF grayling that survived harvest were inherently (genetically) slower growing and did not compensate in growth rate when their faster-growing conspecific competitors were selectively removed by the fishery. That is, growth rate did not increase in spite of the lower population density and, presumably, greater resources available to the surviving fish.

I found no significant differences in the growth rates of MS and MUN grayling: this failed to falsify the null hypothesis. The differences in growth in NF vs ABVCB raise the question of whether fishing caused those differences. The questions in MS vs MUN are: (1) did fishing have no effect on growth rate in these sections; and (2) were the fish in these adjoining sections indeed

separate stocks? I can offer no explanation for the differences in elevation of growth rate curves for MS age 3 vs MUN age 3. It is possible that compensatory growth may occur in these fish because of their high density at the time of recruitment to the fishery. Even if this is the case for age 3 fish, however, it would seem that the lower densities of older fish do not make growth compensation evident.

The trends in growth rates within sections (i.e., within NF and within ABVCB) are more difficult to explain. When a fish population is subjected to harvest, growth rates can: (1) not change; (2) increase (compensate) because of the removal of the more successful competitors (faster growers) so that slower-growing fish can obtain the resources; or (3) appear to decrease, because when faster-growing fish are removed, only those fish that are inherently slow-growing will remain (no growth compensation). In heavily-fished sections (e.g., NF), grayling begin to recruit to the sport fishery (appear in creel censuses) at about age 3, and 200 - 250 mm in length (Hallberg 1980). If the removals of fish that recruit earlier in life (faster growers) were not compensated for by an increase in the growth of the survivors, then the growth rate would appear to decrease between age classes beyond age 3. This decrease was evident in NF grayling. Very few fish of age 5 or greater were found in NF; they

were a small fraction of the stock, and, as a result, less vulnerable (as a group) to fishing. At this point, though, the growth of NF fish began to resemble that of an unfished stock (e.g., ABVCB) in that it showed increases from ages 5 - 6 and 6 - 7. Growth of ABVCB grayling showed increases for ages 4 - 5, 5 - 6 and 6 - 7, and decreases for ages 7 - 8, 8 - 9 and 9 - 10. At this point, explanations become more tenuous.

In sampling a population, I can take only those individuals that have survived competition (intra- and inter-specific), predation, harvest and other mortality. The apparent increase or decrease of growth rates between ages not only reflects which part of the population has survived, but also which part has not remained, because of exploitation or migration. The decrease of growth rates in NF grayling between ages 3 - 4 and 4 - 5 suggest that faster growing fish are less likely to survive because of greater vulnerability to harvest. The apparent increase in growth rates of ABVCB grayling between ages 4 - 5, 5 - 6 and 6 - 7 suggests that intraspecific competition was more important here (faster growers survive), and implies that this competition might have influenced NF grayling, had they not been subjected to fishing. After age 7, however, the pressures on the ABVCB stock seem to change: faster-growing fish are at a disadvantage, and may have high natural mortality, while slower-growing grayling survive.

One might conjecture that this progressive decline of growth rates may be related to the devoting of increasing amounts of metabolic energy to reproduction at these ages, or to a kind of physiological exhaustion of very-fast-growing fish. Based on the evidence available, I can offer no more solid explanation.

The condition of grayling in the larger, slower parts of the river (MS and MUN) was somewhat poorer than that of the grayling in the smaller, faster sections (NF and ABVCB). However, the treatment-and-control experimental design showed no effect of fishing on condition: it failed to falsify the null hypothesis. This might mean that: (1) fishing had no effect on the condition of the surviving grayling; or (2) fishing did have an effect, but the change was compensated for. Might the difference in condition between the NF vs ABVCB pair and the MS vs MUN pair indicate that the smaller, faster parts of the river are better grayling habitat?

Estimates of mortality rates gave the clearest support to any of the alternate hypotheses in this investigation. It seems that fishing contributed considerable mortality in both heavily-fished sections: in NF, the grayling appeared to die at much earlier ages than in ABVCB; MS grayling died at a faster rate than, but over the same ages as, MUN fish. Confounding these observations is

the fact that I cannot be sure if the fish in each of the four sections represent closed populations.

Round whitefish exhibited remarkably similar relative abundances, age-frequencies, growth rates and mortality rates in the NF, MS and MUN sections. This suggests that: (1) the round whitefish in the three sections were all parts of the same stock; or (2) the three sections represent very similar habitat for round whitefish.

Fishing pressure appeared to decrease grayling abundance relative to that of round whitefish. Possible explanations are: (1) a simple decrease of grayling; (2) decrease of grayling plus a competitive increase of round whitefish; or (3) the sections of grayling exploitation are better quality habitats for round whitefish. Because round whitefish exhibited the same abundance, age structure, and rates of growth and mortality in NF, MS and MUN, it would seem that the lower ratio of grayling to round whitefish in NF and MS was due only to a simple decrease of grayling (alternative 1).

The annual migrations of grayling and the gradient of size and age along the East Fork suggest that differential migration may partially or completely account for the differences I observed between heavily- and lightly-fished sections of the Chena River. However, I did not find any gradient of growth rates along the East Fork,

or between the MS and NF sections. This indicates that exploitation is the cause of the growth rate differences I observed in the "treatment-and-control" design. The relative abundance of young, small fish in NF as compared to MS is the opposite of what would be expected if migration was more important than exploitation. On the other hand, although the differences in age-specific survival between MS and MUN grayling are greater than I can account for by migration, the effects of migration and exploitation are not separable in a comparison of survival for MS and NF fish. Therefore, although differential migration is important to Chena River grayling populations (and may be the primary reflector of grayling habitat preferences), I think that the results of this investigation are more attributable to exploitation than to migration.

The gradient of grayling size and age along the East Fork raises further questions. How does this gradient relate to the pre- and post-spawning migrations of grayling? Are the upper parts of the East Fork better habitat for large fish only, or do the large fish exclude the small fish that would otherwise be present, or are large fish the only ones capable of swimming that far during the spring migration(s)? A similar gradient of size exists in the nearby Goodpaster River (Tack 1974). Is this pattern the general rule for grayling in Interior Alaska or for grayling outside central Alaska?

Because of natural variability, any two groups of fish can be expected to exhibit some differences in population dynamics and characteristics. The cogent question here is: "Does fishing cause the observed differences, or are the fish in the two pairs of sections inherently different?"

This question is difficult to answer conclusively based on the evidence available. This was not a strict "treatment-and-control" experiment. As mentioned in the Introduction, the two main obstacles to this investigation were: (1) the lack of assurance of closed populations; and (2) the possibility that some habitat factor(s) were the cause of the differences observed.

Sections NF and ABVCB were widely separated, making any interchange of grayling between them more unlikely than between any other two sections. Indeed, tag returns indicate stability in the grayling stocks. However, this very separation adds weight to the possibility of habitat differences overriding or masking the apparent impact of fishing. I have implicitly assumed a pre-exploitation similarity of NF and ABVCB grayling populations except for differences due to migration and habitat.

The opposite problem exists in comparing MS and MUN: the two sections are more similar in habitat, but the assurance of stock separation is more difficult. Is the

impact of fishing masked or diluted by exchange between the two adjoining sections?

This study cannot fully answer these two questions. However, the salient point is that although the first pair of comparisons is confounded primarily by one problem, and the second pair is confused principally by another problem, fishing apparently has many of the same effects in both sets of comparisons. Therefore, I think that the differences between heavily- and lightly-exploited grayling populations are, in fact, caused by fishing.

In spite of this circumstantial argument, the effects of exploitation on Chena River grayling are far from being completely defined. This investigaton has supplied no concrete before-and-after evidence. A true test of the results of this thesis would be to close the sport fishery completely, and examine the grayling stocks for any changes in population parameters and dynamic rates in formerly heavily-fished sections, still comparing these to the more remote sections. While I cannot suggest a proper duration for such a test, I would expect: more large, old fish to appear in NF and MS; increased individual growth in NF; decreased mortality, increased abundance, and increased ratios of grayling to round whitefish in both NF and MS. Such a test is clearly impractical. Further circumstantial study would be required, and will be outlined later in this section.

The conclusion that fishing is the cause of the observed differences does not automatically imply damage to the stocks. Management may interpret and use this information and analysis to support the present management scheme, or to indicate how a desired change may be accomplished.

The sport fishery on the upper Chena has existed for many years under fairly liberal regulations: a reasonable bag limit but no size restrictions. During recent years, creek censuses (tabulated in Hallberg 1980) have indicated approximate stability in relative abundance (catch-per-angler-hour), relative length-frequencies, average length at capture, and average age at capture, given the yearly fluctuations in recruitment and mortality. More than 60% of the grayling in the creel censuses are of ages 3 and 4, and the average fork length has remained close to 22 cm: anglers are catching many small fish. Previous investigations, as well as this study, indicate that the headwaters of all forks of the Chena contain large fish; these may form a reservoir to support the intensive sport fishery in the Chena River Recreation Area (Hallberg 1978).

This apparent stability of the fishery implies that the effects of fishing on grayling population dynamics have also stabilized and are not increasing. If management should decide that a change in objectives is required, they

may choose to manage for more fish (increased catches) or for larger fish. A more restrictive bag limit might be of help in increasing the overall catch, but since less than 10% of the upper Chena fishermen attain the present bag limit (Holmes 1981), this is not automatically a solution. A minimum size limit may help to increase the size of the fish in the creel and a maximum length limit may improve the recruitment of younger, more catchable fish, but any size restriction should be based on an understanding of the relation between the dynamics and the resultant structure of a stock. Size regulations should not be arbitrary, however, because of the high natural mortality (or emigration) of grayling of recruitment ages (3 and 4), as estimated in MUN. Management would need to balance the numbers of fish of protected ages (sizes) lost to natural mortality during the protected years against the gain in numbers of fish eventually recruiting to the fishery, for example, at age 5.

Closures of time or area would be uncertain remedies, because of our very incomplete understanding of grayling recruitment rates, stock separation, and migration patterns; in the Chena River, and throughout Interior Alaska.

A re-evalution of management objectives would be required in the event of major habitat alterations in the upper Chena, e.g., the current re-opening of heavy gold

mining in the upper East Fork, at Van Curler's Bar. It would be useful to obtain information on recruitment and migration before the mining operation was fully underway, with particular attention to determining the relative contribution of each fork to the sport fishery.

An expansion of the areas accessible to anglers, e.g., a more extensive road system in the Recreation Area, or a higher level of angler effort in the existing system (both distinct possibilities), would also require careful evaluation. The completion of the paving of the upper Chena Hot Springs Road is also likely to increase the impact of angling on the upper Chena River grayling.

In addition to further testing of the present hypotheses, a more complete picture of grayling exploitation dynamics should include the examination of grayling stock separation. Do all Chena grayling belong to one stock? If so, what is the response time of the stock as a whole to a localized impact? If not, where and how are the stocks separated; do they overlap in space or time? To what extent does differential migration cause differences in population dynamics between grayling in different parts of the river?

Related to these questions is an examination of recruitment. Since grayling spawning has been observed almost everywhere in the Chena River (Tack 1974), where do the resulting recruits appear in the fishery? How great is

the role of compensatory recruitment in the maintenance of stock stability? Are there differences in spawning success and recruitment in heavily and lightly exploited sections? Are these differences related to fishing?

What differences in habitat throughout the Chena system might account for the differences in grayling population characteristics that I have observed? At early ages, grayling coexist not only with round whitefish, but also with king salmon; high numbers of each species are present at these early ages. How are resources partitioned among them?

This investigation, like many others, seems to have raised more questions than it has answered. Nevertheless, it has shown some of the ways in which fishing pressure impacts the population dynamics of the Arctic grayling. I hope that this analysis will be useful in the management of the fishery.

SUMMARY

(1) An examination of population dynamics and characteristics was used to quantify the effects of a sport fishery on Arctic grayling in the upper Chena River, in 1979 and 1980. Populations of fish in areas of high and low accessibility to anglers, where accessibility was assumed to be proportional to fishing pressure, were compared in a rough approximation of a treatment and control experiment.

(2) One pair of comparisons (NF vs ABVCB) showed an apparent decrease in grayling abundance, while the other pair (MS vs MUN) showed no effect of fishing on abundance.

(3) Grayling average size and age appeared to decrease in response to exploitation, in both sets of comparisons.

(4) Individual growth rates were significantly different in NF vs ABVCB, showing an apparent decrease in response to fishing pressure. No differences were found in the growth rates of the fish in MS vs MUN.

(5) Trends of growth rates of grayling within, not between, sections were ambiguous.

(6) No effect of fishing on the length-weight relation of grayling was observed.

(7) Fishing pressure apparently contributed considerable mortality to the grayling populations in both heavily-fished sections.

(8) Decreased relative abundance ratios of grayling to round whitefish appear to be attributable to a simple

decrease of grayling, with no increase of round whitefish.

(9) The annual migrations of grayling and the gradient of size and age along the East Fork suggest that differential migration may partially account for the differences I observed between heavily- and lightly-fished river sections. However, I did not find the gradients of growth rate or of relative abundance along the East Fork, or between the two adjacent heavily-fished sections, that I would have expected if differential migration was more important than exploitation in explaining the differences I observed. Nevertheless, a better understanding of grayling habitat preferences and stock separation will be essential in further investigations.

(10) The circumstantial evidence allows the conclusion that the observed differences are, in fact, caused by exploitation.

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